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VOLUME 25
1985-1986

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Volume 25, $8.50 domestic, $9.50 foreign

Copies of *Tulane Studies in Zoology and Botany* sent to regular recipients, if lost in the mails, will be replaced if the editorial offices are notified before the second subsequent issue is released.

COMMUNICATIONS: Address all queries and orders to: Editor, TSZ&B, Department of Biology, Tulane University, New Orleans, Louisiana 70118, U.S.A.
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PRINTED BY E. O. PAINTER PRINTING COMPANY, P. O. BOX 877, DELEON SPRINGS, FLORIDA 32028.

CONTENTS OF VOLUME 25

Number		Page
1.	A REVISION OF THE CENTRAL AMERICAN SPECIES OF BEGONIA SECTION GIREOUDIA (BEGONIACEAE) ..... KATHLEEN BURT-UTLEY	1
2.	SYSTEMATICS OF THE KEY SILVERSIDE, MENIDIA CONCHORUM, WITH COMMENTS ON OTHER MENIDIA SPECIES (PISCES: ATHERINIDAE) ..... CHARLES F. DUGGINS JR., ALVAN A KARLIN, KENNETH RELYEA, AND RALPH W. YERGER	133
	GEOGRAPHIC VARIATION IN GULF SLOPE POPULATIONS OF THE BLUNTNOSE DARTER, ETHEOSTOMA CHLOROSOMUM (HAY) ..... HENRY L. BART JR. AND ROBERT C. CASHNER	151

TULANE STUDIES IN ZOOLOGY AND BOTANY
VOLUME 25
INDEX TO SCIENTIFIC NAMES

Begonia, 3-129
acutiloba, 119
barsalouxii, 120
broussonetiifolia, 49
buseyi, 119
calderonii, 120
cardiocarpa, 86
carpinifolia, 120
conchifolia, 120
confusa, 121
corredorana, 46
crassicaulis, 94
croatii, 64
dressleri, 115
fonsecae, 111
fusca, 57
garagarana, 55
heracleifolia, 89
involucrata, 51
louis-williamsii, 72
ludicra, 121
manicata, 82
morii, 74
multinervia, 38
nelumbiifolia, 76
phyllomaniaca, 122
pinetorum, 113
plebega, 102
pruinata, 122
quaternata, 66
sartorii, 42
sericoneura, 97
setulosa, 122
strigillosa, 68
thiemei, 80
urophylla, 59
vitifolia, 121
Begonia sect. *Casparya*, 125
Sect. *Begonia*, 127
Sect. *Doratometra*, 127
Sect. *Gireoudia*, 126
Sect. *Hexaptera*, 126
Sect. *Knesebeckia*, 126
Sect. *Liebmannia*, 126
Sect. *Podandra*, 126
Sect. *Pritzelia*, 126
Sect. *Ruizopavonia*, 126
Sect. *Scheidweileria*, 128
Sect. *Steineria*, 127
Sect. *Urniformia*, 127
Sect. *Weilbachia*, 126
Etheostoma, 151-169
chlorosomum, 151-169
davisoni, 151-169
Menidia, 133-149
audens, 135
beryllina, 133-149
clarkhubbsi, 135
colei, 133-149
conchorum, 133-149
extensa, 133
menidia, 133-149
peninsulae, 133-149
Menidiella, 133

TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 25, Number 1 $5.50 July 5, 1985

A REVISION OF CENTRAL AMERICAN SPECIES OF BEGONIA SECTION GIREOUDIA (BEGONIACEAE)

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Errata

Tulane Studies in Zoology and Botany Volume 22, Pages 67-84.—

HEINS, D. C. 1981. Life history pattern of *Notropis sabinae* (Pisces: Cyprinidae) in the lower Sabine River drainage of Louisiana and Texas. Tulane Studies in Zoology and Botany 22: 67-84.

The page proofs for this paper included a number of errors which were noted on them by the author. However, the corrections were not made prior to publication. The more important errors are listed below.

Page 69, STUDY AREAS, par. 2, line 8, *"range"* should be *"ranging"*

Page 71, right column, line 3, *"dital"* should be *"distal"* and *"hevily"* should be *"heavily"*

Page 72, right column, par. 2, lines 10-11, *"distributions"* should be *"distribution"*

Page 74, left column, par. 1, line 16, *"(S=0.0452)"* should be *"(s=0.0452)"*

Page 74, left column, par. 2, line 10, "X^2" should be "X_c^2"

Page 76, right column, line 12, insert "$\geq$" so that the line reads, *"individuals (particularly those $\geq$ 44 mm"*

Page 77, the table is the first half of Table 2 which ends on page 78; the *legend* for this table is on page 78

Page 78, table legend, line 2, insert "$\geq$" within the parenthesis which should read "*($\geq$ 33 mm SL)*"

Pages 81-82, references to *"Heins et al., in press"* should be *"Heins et al., 1980"*

Page 83, LITERATURE CITED, the reference for *Moore (1968)* is out of order and should appear after the reference for *Hubbs and Walker (1942)*

TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 25, Number 1 $5.50 July 5, 1985

A Revision of Central American Species of Begonia section Gireoudia (Begoniaceae)

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CONTENTS

Introduction 3
Taxonomic History 4
Intersectional Relationships 5
Distribution and Habitat 7
Morphology 10
Habit 10
Vestiture 11
Leaves 14
Inflorescences 18
Bracts 20
Floral Morphology 21
Capsules 25
Seeds 26
Breeding System and Hybridization 26
Intrasectional Relationships 29
Taxonomic Treatment 32
Explanation of Key 33
Key to Central American Species of *Begonia* sect. *Gireoudia* 34
1. *B. multinervia* 38
2. *B. sartorii* 42
3. *B. corredorana* 46
4. *B. broussonetiifolia* 49
5. *B. involucrata* 51
6. *B. garagarana* 55
7. *B. fusca* 57
8. *B. urophylla* 59
9. *B. croatii* 64
10. *B. quaternata* 66
11. *B. strigillosa* 68
12. *B. louis-williamsii* 72
13. *B. morii* 74
14. *B. nelumbiifolia* 76
15. *B. thiemei* 80
16. *B. manicata* 82
17. *B. cardiocarpa* 86
18. *B. heracleifolia* 89
19. *B. crassicaulis* 94
20. *B. sericoneura* 97

21. *B. plebeja* 102
22. *B. conchifolia* 108
23. *B. fonsecae* 111
24. *B. pinetorum* 113
25. *B. dressleri* 115
26. *B. buseyi* 117
Doubtful and Excluded Species 119
Appendix I: Species in sect. *Gireoudia* occurring in Mexico, Central America and South America 123
Appendix II: Key to Central American Sections of *Begonia* 125
Appendix III: Synopsis of Central American *Begonia* Sections 125
Acknowledgments 128
Resumen 129
Literature Cited 129

Abstract

Begonia sect. *Gireoudia* is the largest of 14 *Begonia* sections occurring in Central America. It is a phenetically related group of species that can be differentiated from other sections by plant habit coupled with floral morphology. Of the 26 species herein recognized from Central America, 16 are endemic to the region, largely to Costa Rica and Panama where they range from sea level to over 2000 m elevation.

Species within *Begonia* sect. *Gireoudia* from Central America were reevaluated, based upon information from field work and an examination of available herbarium specimens, including types. Five new species were recognized among the 26 species in sect. *Gireoudia* that occur in Central America; of these, four were Panamanian and one was Guatemalan. Two widely ranging and frequently collected taxa, *B. sericoneura*, and *B. urophylla* have been reinterpreted as a result of this research, while two additional species, *B. broussonetiifolia* and *B. cardiocarpa* which were treated in synonomy in recent floras, are recognized as distinct. Accompanying this treatment are discussions of morphological characters important in distinguishing species in sect. *Gireoudia* and illustrations of major floral and vegetative characters. A detailed key to Central American species in the section is included. Each species is accompanied by a thorough description of its morphological features along with a discussion of its relationships to other taxa in the section from Central America. Tables were prepared to compare phenetically similar taxa and distribution maps are included for all species. Recently described species are illustrated with line drawings. Species were divided into 13 species groups based upon morphological similarities among taxa.

Introduction

Begonia is one of the largest genera of flowering plants and is represented in the Neotropics by almost 600 species which are distributed from Mexico to southern South America. The genus is characterized by a pervasive asymmetry of leaf form, generally succulent petioles, unisexual flowers that are borne within the same inflorescence, and winged capsules. Because of the foregoing suite of characters, most begonias are readily identified to genus even by untrained horticultural enthusiasts, but species determinations can be difficult even for the systematist due to many morphological similarities among taxa. These phenetic similarities prompted Candolle (1859) to deplore the division of *Begonia* into 33 and later 41 genera by Klotzsch (1854, 1855) and propose that differences among taxa be recognized at the sectional level. While *Begonia* appears to be phenetically cohesive, the relationships among taxa within *Begonia* remain poorly understood and infrequently studied. The problems with *Begonia* are compounded by the lack of a modern treatise for the genus. The last comprehensive monograph of the genus was the treatment of the Begoniaceae for the Prodromus (Candolle, 1864).

Since 1925 the major thrust of research in Neotropical and Old World *Begonia* has been directed toward regional floristic surveys, with the resulting recognition of numerous new taxa both at the sectional and specific level with little attempt to discuss relationships among taxa or, in some treatments, to identify sectional affinities. Irmscher (1949, 1953) occasionally provided brief discussions of some South American sections to accompany his new species descriptions. Floristic treatments of the Begoniaceae presently exist for many Latin American regions, including Ar-

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gentina (Smith and Schubert, 1941), Santa Catarina, Brasil (Smith and Smith, 1971), Bolivia (Smith and Schubert, 1945), Colombia (Smith and Schubert, 1946b), Costa Rica (Standley, 1937), Peru (Smith and Schubert, 1941), Panama (Smith and Schubert, 1958) and Guatemala (Smith and Schubert, 1961). Smith and Wasshausen (1979) recently prepared a brief revision of *Begonia* for Ecuador, prior to a more comprehensive treatment for the Flora of Ecuador project. There are presently some 54 Neotropical sections comprising over 600 species, of which 18 sections are Middle American and include over 120 species. Many recently described Neotropical sections are monotypic.

While a revisionary study of Neotropical *Begonia* is long overdue, the very size of the group (+ 600 spp) mitigates against any revision directed at the genus as a whole. However, many sections within the genus appear to be phenetically and geographically cohesive units that are only superficially understood from floristic surveys and await more detailed systematic research. A good example of this is found in *Begonia* sect. *Gireoudia*, one of 18 sections occurring in Mexico and Central America (Appendix II, Appendix III). Section *Gireoudia*, with the exception of a few wide ranging species that extend into northern South America, is restricted to Mexico and Central America. It is the largest *Begonia* section occurring in Central America with 26 recognized species and forms a morphologically coherent group of species within *Begonia* that can be distinguished readily from other sections in the Neotropics on the basis of plant habit, leaf form and floral morphology. *Begonia* species in section *Gireoudia* are predominantly rhizomatous perennials with oblique to transverse, palmately nerved leaf blades, but may infrequently be suffrutescent herbs or have straight leaf blades. In sect. *Gireoudia* both staminate and pistillate flowers typically possess two sepals, while lacking petals. Moreover, in the pistillate flowers, ovaries are typically three-locular with bilamellate placentae. The three styles are weakly to strongly fused and are terminated by lunate to bicornute stigmas where the receptive surface is restricted to a narrow papillaceous band extending the length of the stigma. Along with morphological similarities, species within sect. *Gireoudia* appear to be cytologically homogeneous. Of the 34 putative species that Legro and Doorenbos have studied, all have diploid chromosome numbers of 28 (Legro and Doorenbos, 1969, 1971, 1973).

Taxonomic History

The genus *Gireoudia* was first distinguished by Klotzsch (1854) based on its two-"tepaled" staminate and pistillate flowers, bilamellate placentae, reniform stigmas, linear-oblong basally attenuate anthers and often bracteolate pistillate flowers. In his treatment of the Begoniaceae Klotzsch (1855) included 28 species within *Gireoudia*, most of which had been described previously in *Begonia*. Although Alphonse de Candolle (1859) reduced *Gireoudia* and many other of Klotzsch's genera to sectional status, he recognized the merit of the distinguishing features that Klotzsch selected and utilized them in his own sectional delimitations. In his treatment for the Prodromus, Alphonse de Candolle (1864) recognized 33 species within *Gireoudia* and he emended Klotzsch's description to include species with staminate flowers which occasionally had two petals. He also recognized that not all species in the section had pistillate flowers with reniform (lunate) stigmas. Both Warburg

(1894) and Irmscher (1925) treated sect. *Gireoudia* along with sections *Rachia* and *Psathuron* as subsections of sect. *Magnusia*. Although both *Gireoudia* and *Magnusia* were part of Klotzsch's conspectus (1854), *Magnusia* was not treated as a section of *Begonia* until 1865 (Candolle, 1864). Thus, if sections *Gireoudia* and *Magnusia* are considered taxonomically synonymous, sect. *Gireoudia* has priority since it was recognized first at the sectional level within *Begonia*. Alphonse de Candolle's treatment of sect. *Gireoudia* constituted the last monographic work within the section. Species in sect. *Gireoudia* have most recently been studied in the context of various regional floras (Standley, 1937; Smith and Schubert, 1958, 1961). As currently recognized sect. *Gireoudia* encompasses sections *Magnusia* and *Psathuron* but not sect. *Rachia*, a taxon which was recently treated in sect. *Knesebeckia* (Irmscher, 1960). Section *Rachia* shares with sect. *Knesebeckia* staminate flowers with two sepals and two petals but its pistillate have 2 sepals and a petal, unlike the generally 3-5 tepaled pistillate flowers most species in of sect. *Knesebeckia*. Also included in sect. *Gireoudia* is sect. *Auriformia* which was described as having entire placentae. However, an examination of *B. bakeri* failed to confirm that the placentae were entire. In all capsules examined the placentae were bipartite and in critical characters, *B. bakeri* is essentially indistinguishable from *B. cardiocarpa* which is treated in sect. *Gireoudia*. This situation is further addressed in the discussion of *B. cardiocarpa*.

Intersectional Relationships

Begonia is pantropical in its distribution, but is most abundant in the Far East and Neotropics. Irmscher (1925) recognized two broad centers of diversity for the genus, the first of which ranges from Mexico to the Andes and Brazil, while the second spans the eastern Himalayas, mountains of Indochina, Malay Archipelago, the Philippines and New Guinea. Both sect. *Begonia* and sect. *Knesebeckia* occur in the Far East and in the Neotropics from Mexico to South America. *Begonia* is thought to have migrated into North America from South America as early as the Eocene (Raven and Axelrod, 1974) and some Middle American sections including sect. *Gireoudia* may have arisen from this ancestral stock.

Klotzsch (1854, 1855) revolutionized the approach to *Begonia* systematics when he divided *Begonia* first into 33 and then 41 distinct genera which he circumscribed using primarily floral characters that included the numbers of perianth parts in staminate and pistillate flowers, anther shape, stigma shape, distribution of stigmatic papillae, placental lobes, locule number and style persistence. Klotzsch employed this latter character, coupled with capsular differences, to separate the Begoniaceae into two subfamilies (as suborders), the Stephanocarpeae, characterized by persistent styles and membranaceous, and triangular capsules dehiscing through arcuate fissures and the Gymnocarpeae, characterized by deciduous styles and somewhat cartilaginous turbinate capsules with dehiscence through the wings. Klotzsch placed the majority of genera (33) into two tribes, the Begonieae and Pritzelieae within the subfamily Stephanocarpeae. Klotzsch's use of style persistence as a primary character to delimit subfamilies was questioned by Alphonse de Candolle (1859) who realized that it was an unreliable character since abscission of styles within an inflorescence is apparently a random

event. Although Candolle (1859, 1864) treated most genera Klotzsch described as sections within *Begonia,* he recognized the merit of many characters Klotzsch utilized and the importance of Klotzsch's contribution toward an understanding of the genus. Many sections have restricted geographical distributions and represent groups of phenetically similar taxa. Candolle (1859, 1864) maintained both *Casparya,* distinguished from *Begonia* by its loculicidal dehiscence through the horns or capsule wings, and *Mezieria,* with parietal placentation, as distinct genera in the Begoniaceae. Warburg (1894) and Irmscher (1925) revised some sectional concepts and provided synopses of the sections, including both *Casparya* and *Mezieria* which Candolle had maintained as distinct, but declined to establish subgenera or other suprasectional taxa. In Irmscher's treatment, 60 sections were recognized within *Begonia,* the majority of which (33) were Neotropical. His key to the sections, which is still utilized today (Smith and Wasshausen, 1979), followed Candolle's (1864) in dividing sections first into major geographical regions, Africa, Asia and the Neotropics. Due to the absence of recent monographic research in *Begonia,* it is impossible to assess the relationships among Neotropical sections within the scope of this project.

While the Neotropical sections desperately need revisionary study, many appear to be morphologically, cytologically and geographically coherent. A key to the Central American sections of *Begonia* along with a brief synopsis of each section is presented in Appendices II and III. Section *Gireoudia* forms a geographically and phenetically cohesive unit within *Begonia* that can be distinguished from other Neotropical sections on the basis of floral morphology coupled with plant habit and leaf form. Among Mexican and Central American sections, sect. *Gireoudia* appears closely allied with sect. *Weilbachia,* with which it shares similar growth forms, blade form, villous to squamose induments, and apetalous flowers. These sections also have similar chromosome numbers, with $2n=28$ (Legro and Doorenbos, 1969; 1971). The most conspicuous differences between the sections involve locule number and capsule orientation. Ovaries of species within sect. *Gireoudia* are characteristically trilocular while the capsules are only inclined, but in sect. *Weilbachia* ovaries are bilocular and the capsules strongly nutant. Candolle (1864) associated sect. *Gireoudia* with sect. *Knesebeckia* because of similarities in styles, anthers and overlapping distributions in Middle America. He also considered sect. *Rachia,* which Irmscher (1960) included in sect. *Knesebeckia,* to be intermediate between these two sections. Both taxa also share the same chromosome number, $2n=28$ (Legro and Doorenbos, 1969). They differ from each other in the arrangement of stamens and in the number of floral parts in both pistillate and staminate flowers, with sect. *Knesebeckia* characteristically having staminate flowers with monadelphous stamens, two sepals and two petals and pistillate flowers with five or rarely three or four tepals. Species within sect. *Knesebeckia* are primarily herbs or suffrutescent herbs, in contrast to species in sect. *Gireoudia* that are primarily rhizomatous herbs and only infrequently suffrutescent herbs. Section *Knesebeckia* was included in sect. *Begonia* (as sect. *Begoniastrum* A.DC.) by Warburg (1894) and Irmscher (1925) because both taxa have similar herbaceous to suffrutescent habits, frequently produce bulbils in the axils of their leaves, have staminate flowers with two petals and two sepals

and pistillate flowers with generally five tepals. These sections differ from each other primarily in the arrangement of their stamens which are monadelphous in sect. *Knesebeckia* but free in sect. *Begonia*. As Warburg (1894) circumscribed sect. *Begonia*, it was restricted to the Neotropics. Those species from the Far East which had been included in sect. *Knesebeckia* by Klotzsch (1854) and Candolle (1864), Warburg placed in sect. *Diploclinium* (Wight) A.D.C. in their own subsection, *Knesebeckiopsis* Warbg. Irmscher (1925), however, considered sect. *Diploclinium* to consist solely of species with bilocular ovaries and treated the Far Eastern taxa, which Warburg had placed in sect. *Diploclinum*, in sect. *Begonia*. In a recent survey of cultivated begonias, Irmscher (1960) considered sect. *Knesebeckia* to be distinct from sect. *Begonia*.

The apetalous flowers of species in sect. *Gireoudia* are a primary character with distinguishes sect. *Gireoudia* from most other *Begonia* sections. Only nine other sections have apetalous staminate and pistillate flowers with two sepals; of these, only four are Neotropical in their distribution (*Liebmannia, Rossmannia* (Kl.) A.DC., *Ruizopavonia* and *Weilbachia*). In contrast, the vast majority of *Begonia* sections have staminate flowers with two sepals and two petals, and pistillate flowers with five tepals. Aside from a superficial floral similarity resulting from the apetalous condition, major differences in floral structure, leaf form or habit exist between sect. *Gireoudia* and the four other Neotropical sections. The three-locular erect or inclined capsules of species in sect. *Gireoudia* unequivocally distinguish it from both sect. *Liebmannia* and sect. *Weilbachia* whose species possess two-locular, strongly nutant capsules. Section *Gireoudia* differs strongly from sect. *Ruizopavonia* in both stigma form and in the distribution of papillae on the styles and stigmas. Unlike sect. *Gireoudia*, the stigmas in sect. *Ruizopavonia* are deeply divided and often even secondarily divided. Not only are the stigmas papillaceous in sect. *Ruizopavonia* but also the stylar surface is covered with minute papillae. Section *Gireoudia* is also readily distinguished from sect. *Ruizopavonia* and sect. *Rossmannia* by the criteria of plant habit and leaf morphology. Both of these latter taxa are comprised of species which are suffrutescent herbs and possess generally straight, but asymmetric, pinnately nerved leaves. The primary character which separates sect. *Gireoudia* from the remaining five Old World sections are the bipartite placentae in sect. *Gireoudia* versus the entire placentae in these Old World sections.

Distribution and Habitat

Begonia sect. *Gireoudia* ranges from the states of Durango, Sinaloa and Tamaulipas in Mexico throughout Central America and into Colombia and Venezuela in northern South America. No species in the group are endemic to South America, and the three taxa occurring there are widely distributed throughout Mexico and Central America. Species in sect. *Gireoudia* are most numerous in Mexico where 36 taxa are known, and of these, 67% are endemic, primarily to the states of Oaxaca and Chiapas. With few exceptions, Mexican species remain poorly known and poorly collected.

In Central America, sect. *Gireoudia* is best represented in Panama where 16 species are found. Excluding Mexico, Panama has the highest level of endemism in section (5 spp.; 32%). Another four taxa are restricted to Costa Rica

and Panama. Next to Panama the greatest concentration of species occurs in Guatemala (14 spp.; 1 endemic) while sect. *Gireoudia* is poorly represented in Nicaragua (6 spp.; no endemics) and Honduras (8 spp.; 1 endemic). Only a few widely distributed taxa are known from Belize and El Salvador. A list of species in each country is presented in Appendix I. Several distribution patterns are interesting and deserve further recognition. Although *B. nelumbiifolia* is widely distributed, ranging from Mexico to northern South America, it is unknown from Honduras, Nicaragua, and western Panama. Also lacking from the floras of Nicaragua and Honduras are *B. strigillosa* and *B. urophylla* which extend from Mexico to Panama and from Guatemala to northern South America, respectively. These patterns of disjunction may result from the limited number of collections from wet montane areas in Nicaragua and Honduras. Species in sect. *Gireoudia* presently known from these countries are adapted primarily to drier climatic conditions. Three species abundant and widespread in Costa Rica, *viz. B. multinervia, B. sericoneura* and *B. strigillosa,* have only rarely been collected from adjacent Panama. The poor representation of *B. sericoneura* in Panama was unexpected because it is one of the most widely distributed species in sect. *Gireoudia* and is well-collected in Colombia. The restricted distribution of *B. multinervia* appears anomalous because it occurs in wet tropical forests along the Caribbean coast which are presently continuous from Mexico to Costa Rica and western Panama. This species is also common in the Valle del General and on the lower Pacific slopes of the Talamancas and Fila Cal in southern Costa Rica.

All but four species from sect. *Gireoudia* in this study flower during the dry season which extends from December to April in Central America (Vivo Escoto, 1964), and when the rainy season commences in late April or May, most species have mature or maturing capsules, thus providing optimum conditions for pollination and subsequent seedling establishment. *Begonia fusca* and *B. fonsecae* do not appear to exhibit a distinct flowering season, while *B. plebeja* and *B. strigillosa* flower profusely during the latter part of the rainy season from September to December.

Species within sect. *Gireoudia* occur primarily in forested areas from sea level to 3000 m elevation (Fig. 1). Almost two thirds of the species have been collected at elevations less than 1000 m while a third occur above 2000 m elevation. Most species have broad elevational ranges that span 600-1000 m, but several species have even wider distributions that approach 2000 m elevation.

Species in sect. *Gireoudia* are most abundant in wet forests throughout Mexico and Central America where they frequently colonize steep slopes and areas above streams. Only a few Central American species in the section, however, have been reported from rainforest life zones as recognized by Holdridge et al. (1971). Within forested areas rhizomatous species often occur on tree trunks and rocks, habitats that are devoid of most other flowering plants, while the suffrutescent species are only rarely epiphytic or saxicolous. Only a few species such as *B. heracleifolia, B. multinervia* and *B. urophylla* are successful in colonizing generally seasonally wet, open roadbanks where they may form large populations. Several species, including *B. crassicaulis, B. heracleifolia* and *B. plebeja,* are adapted to growing in seasonally dry, deciduous forests throughout Central America and tolerate high levels of insolation. Most taxa form ex-

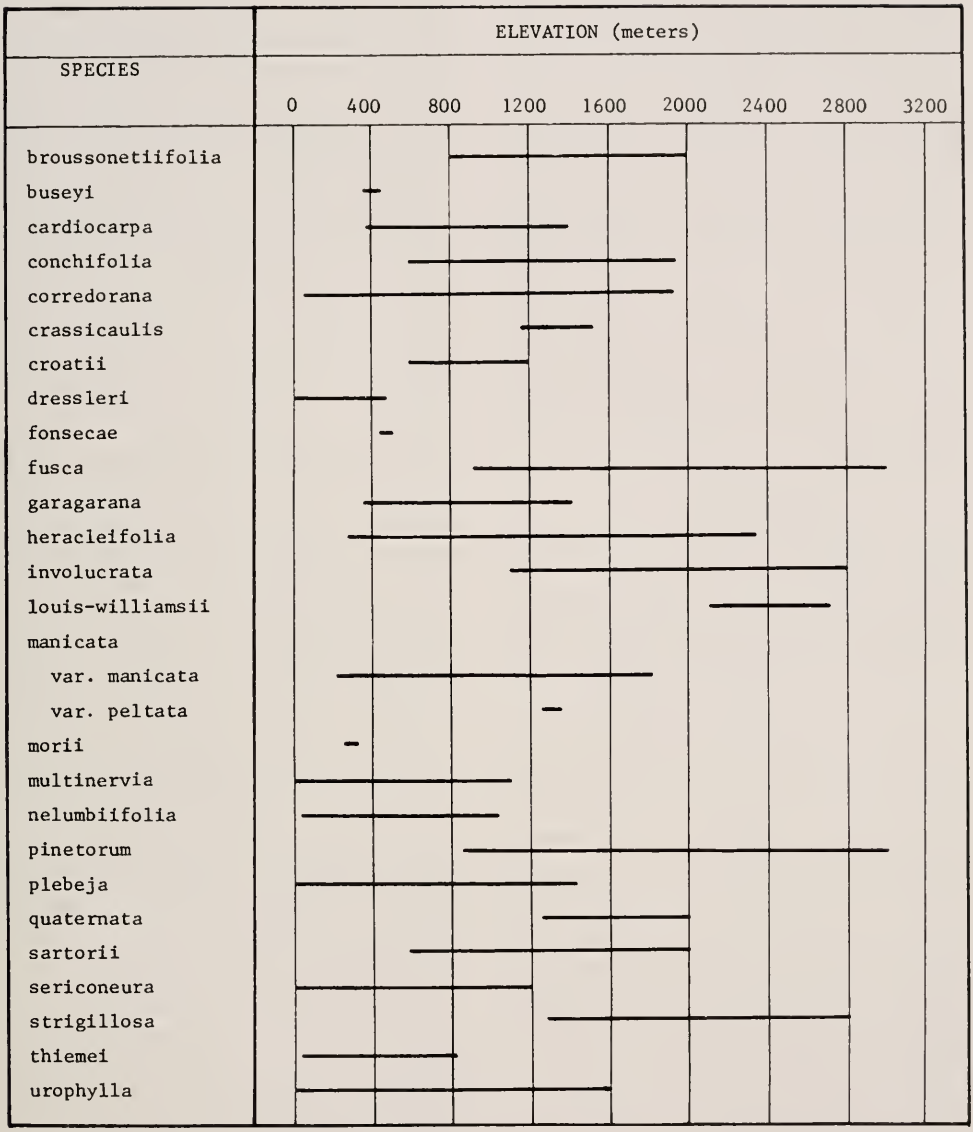

Fig. 1. Elevational distribution of the Central American species of *Begonia* sect. *Gireoudia*.

tremely local populations that range in size from a few to hundreds of individuals. These localized populations may result from poor seed dispersal. Although a number of species are widely distributed and begonias are thought to be readily dispersed (Raven and Axelrod, 1974), most begonias lack specific adaptations for dispersal. Their winged capsules may function primarily to enhance seed expulsion by increasing capsular motion in wind (Pijl, 1972). For actual dispersal seeds must rely on animal vectors that inadvertently come in contact with them or climatic factors like wind or rain. While wind is an important dispersal agent for lighter seeds, it is particularly significant in exposed

habitats (Levin and Kerster, 1974). The effectiveness of wind as a dispersal agent for *Begonia* will be reduced in dense forest habitats associated with many species, but may be the primary factor in the dispersal of seeds from populations in exposed areas or in deciduous forests. Although most species are usually found in isolated populations, it is not uncommon to find two or more species in sect. *Gireoudia* growing sympatrically and occupying the same habitats because species have broad elevational distributions and frequently similar habitat preferences.

Morphology

Habit. Species in sect. *Gireoudia* are either acaulescent or caulescent, long-lived perennials and can be divided into two distinct morphological groups based on whether the plants are suffrutescent with erect stems or are rhizomatous. Only five of the 26 Central American species in sect. *Gireoudia* are suffrutescent herbs (*B. broussonetiifolia, B. corredorana, B. involucrata, B. multinervia, B. sartorii*), the remaining 21 species are caulescent or acaulescent rhizomatous herbs. The erect or ascending stems or "canes" of suffrutescent species are elongate and unbranched, or only sparingly branched, reaching 1-3 m long. Rarely when these species are growing in dense forests on steep slopes, their stems may become declined or sprawling. An individual plant consists of numerous fastigiate stems, with new stems arising from the rootstock or bases of older stems. Internodes are usually elongate, but within a single stem can vary significantly in length, possibly resulting from differences in available light or moisture during the growing period. The internodes are often strongly lenticellate and range from villous to pilose or tomentose in indument but are never squamose.

Within the rhizomatous species two different growth forms are prevalent, depending upon rhizome orientation which may be characterized as erect to ascending in one group and repent in the other. In both groups, rhizome growth is indeterminate, with older portions of the rhizome gradually senescing and dying. The older parts particularly are often infected with borers. Of the 21 rhizomatous species in Central America, only four have generally ascending rhizomes, *B. crassicaulis, B. cardiocarpa, B. manicata* and *B. sericoneura*. However, when specimens of these species are very young, their rhizomes may be repent and acaulescent, but with elongation they become more or less vertically oriented and caulescent. In *B. manicata* and *B. cardiocarpa*, the internodes become somewhat elongate, reaching 3 cm. In these species and *B. sericoneura*, as the rhizome of an individual plant becomes excessively elongate, it gradually becomes declined distally and with further growth becomes decumbent, rooting where it comes in contact with its substrate. Once the rhizome establishes new roots, further growth is oriented upwards. Within these species the rhizomes are often thick and succulent, with large quantities of pith parenchyma and may function as moisture reservoirs enabling the species to endure prolonged dry seasons in exposed habitats. With age rhizomes become silver-gray or silver-brown, a coloration which may be important in reflecting incident radiation, thereby helping to maintain a lower internal rhizome temperature. Growth in *B. cardiocarpa* and *B. sericoneura* can exceed 50 cm a year under favorable conditions. In *B. crassicaulis* and many populations of *B. sericoneura*, growth exhibits periodicity, ceasing during the dry season when flowering occurs. Similar periodicity has been observed in *B.*

sericoneura maintained under greenhouse conditions. In contrast *Begonia cardiocarpa* appears to grow continuously both in the wild and in cultivation. The internodal indument of these taxa may be squamose (*B. manicata*) or coarsely villous resulting from a mixture of coarse whiplash trichomes and barbate trichomes (*B. cardiocarpa, B. crassicaulis* and *B. sericoneura*).

The largest group of species in sect. *Gireoudia* has characteristically repent rhizomes that are acaulescent or rarely caulescent. Internodes are generally short, but occasionally may become elongate and have squamose, coarsely villous, villous or villous-squamose indu-ments. Only one species, *B. garagarana*, is characterized by its caulescent rhizomes with elongate internodes, but several populations of *B. strigillosa* from Guatemala have caulescent rhizomes much like runners. Rhizomes are frequently unbranched or only sparingly branched, but *B. conchifolia* and *B. plebeja* have rhizomes that branch freely, forming dense mats on rocks and tree trunks. Some species including *B. heracleifolia, B. pinetorum* and *B. plebeja* have thick, succulent rhizomes which, like the rhizomes of *B. sericoneura*, may function as means of drought avoidance enabling these species to colonize seasonally dry, inhospitable habitats. Growth in many of the repent, rhizomatous species is continuous throughout the year, but certain species including *B. plebeja* and some populations of *B. heracleifolia* display periodicity that is maintained even under favorable greenhouse conditions.

Although all species in sect. *Gireoudia* grow terrestrially, most are capable of exploiting epiphytic or saxicolous habitats and will frequently occupy all three habitats within the same general locality, e.g. *B. sericoneura* and *B. strigillosa*. It is likely that the modifications which have occurred in the stem and the relationship between stem and leaves are largely responsible for the ability of the rhizomatous species to colonize a diversity of habitats that most angiosperm groups find unsuitable. Those individuals which grow epiphytically tend to colonize bases of tree trunks, but not higher, more exposed canopy situations. The rhizomatous species are frequently successful in colonizing rocks in dense forests and also areas of potentially high insolation. While it appears that most, if not all, rhizomatous species grow both saxicolously and epiphytically, epiphytism is rare among the suffrutescent species, having been observed in only one, *B. broussonetiifolia*. These species may occasionally grow among rock crevices where detritus has accumulated, but are most abundant in terrestrial habitats with sufficient moisture.

Vestiture: The importance of *Begonia* trichomes to systematics was recognized by both Fellerer (1892) and Solereder (1908). Species in sect. *Gireoudia* display a diversity of trichome forms which, when coupled with differences in tricome density, provide important characters that can be used in species delimitation. While trichomes occur on most vegetative and reproductive parts, internodal and petiolar induments are particularly useful taxonomically. Although trichome density may vary within species, certain taxa, *viz. B. garagarana* and *B. thiemei*, typically have very sparse induments, while other species including *B. pinetorum* are densely tomentose. Two basic trichome forms have been recognized in *Begonia*, glandular or capitate hairs (Figs. 2A, B) and multiseriate hairs (Figs. 2C-F) which include shaggy hairs or villi and whiplash trichomes (Fellerer, 1892). While shaggy hairs can be described simply as coarse

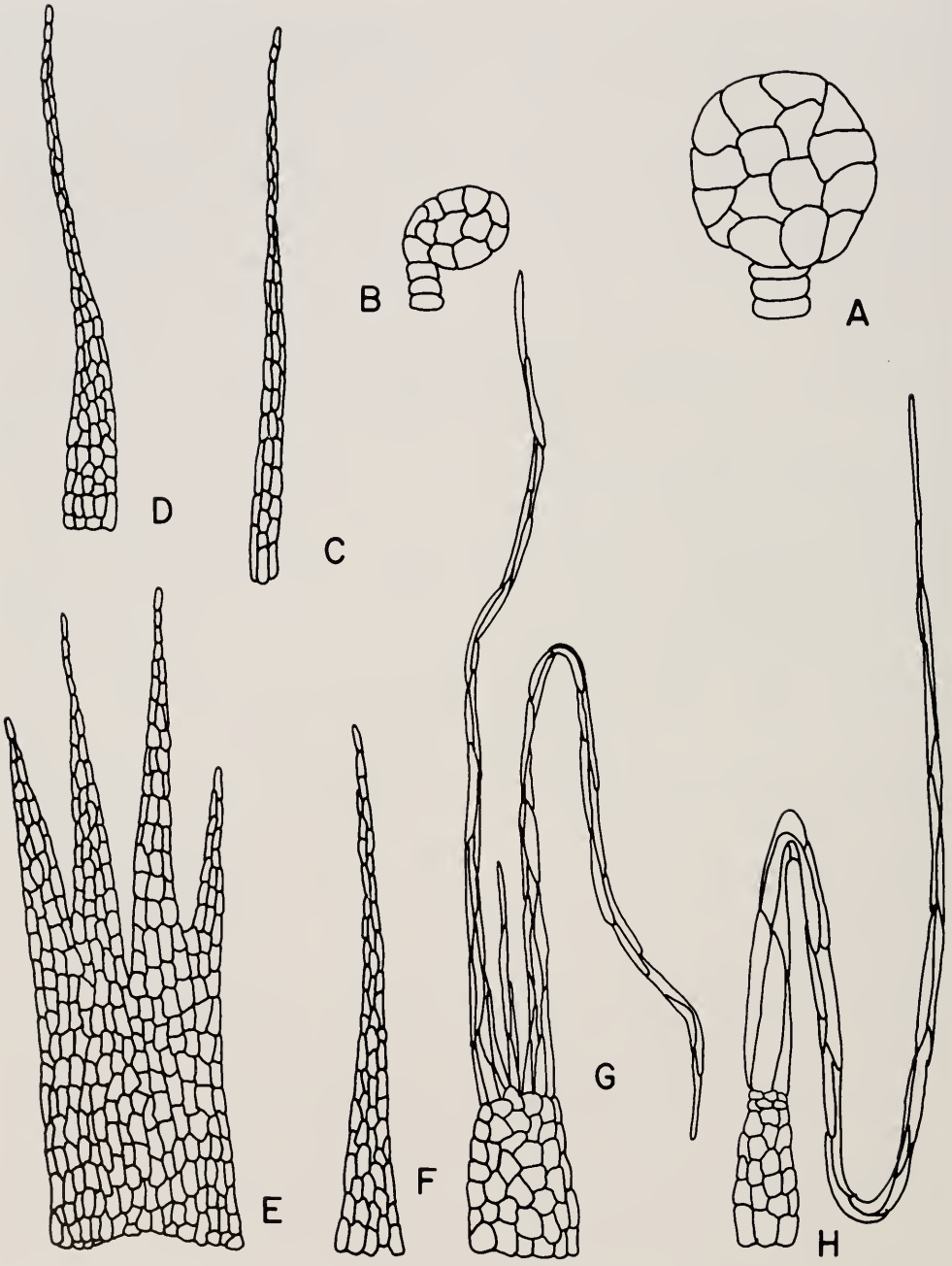

Fig. 2. Representative trichome types in sect. *Gireoudia*. A. Pearl gland. B. Glandular hair. C-D Villi. E-F Scales. G. Barbate trichome. H. Whiplash trichome.

trichomes on *Begonia* petioles (Payne, 1978), they include a range of trichome types, the most conspicuous of which is the broad lacerate scale. Several trichome types appear intermediate between true scales as typified by those of *B. urophylla* or *B. manicata* and whiplash trichomes observed on petioles of *B. sericoneura* and a few other taxa and are herein referred to as barbate trichomes. The remaining group of undifferentiated multiseriate trichomes are termed villi.

Because of their widespread distribution within *Begonia,* villi are here thought to represent a primitive condition from which both lacerate scales and whiplash trichomes are derived. Villi occur on almost half the Central American species in sect. *Gireoudia* and, on petioles of some species, it is not unusual to observe very narrow, entire flat scales intermixed with the villi. Scales appear to have arisen repeatedly in Begonia, occurring in a number of sections (Fellerer, 1892) and in sect. *Gireoudia* four rhizomatous species from Central America have squamose petiolar indu-ments, while two others, *B. heracleifolia* and *B. strigillosa,* have induments ranging from squamose to villous-squamose. None of the suffrutescent species, however, are squamose. Among these species the trichomes are frequently living at maturity and are translucent white or, as in *B. manicata,* deeply pigmented with anthocyanins. Almost a third of the species are characterized by whiplash trichomes, a type of trichome that only occurs in a few other *Begonia* sections (Fellerer, 1892). Villi modified distally or basally can superficially resemble whiplash trichomes.

To determine the trichome type present, it is often necessary to prepare slides for microscopic examination. In some species, however, trichome form was unequivocally determined only when slides were prepared from living material. This resulted in a reinterpretation of the trichomes characteristic of *B. nelumbiifolia* and *B. involucrata.* Fellerer (1892) reported villi for both these taxa, but more recent examination has revealed that their induments are formed from whiplash trichomes.

a. Glandular Trichomes.

Glandular trichomes occur on most plant parts and have been observed in all species of sect. *Gireoudia,* but because of their very small size (usually shorter than 0.1 mm) they are often overlooked. Included here also are pearl glands which appear like small transparent globules and may contain aliphatic oils (Uphof, 1962). Both glandular trichomes and pearl glands consist of small globose to subglobose heads and multicellular stalks (Figs. 2A, B). As there is a tendency for the heads of pearl glands to disarticulate, they are frequently missing or less dense on older plant parts of preserved specimens. In general, no particular taxonomic significance is attached to the presence or distribution of glandular hairs among plant parts because of their common occurrence throughout the section. Only one species, *B. heracleifolia,* has bracts which are unusual by being glandular-serrulate marginally.

b. Villi.

Villi encompass a variety of entire, multiseriate trichomes containing cells of relatively uniform size (Figs. 2C, D). In some species these trichomes often become uniseriate distally. Villi also exhibit a tendency to develop more elongate cells distally, and when this happens they resemble whiplash trichomes. While

a villous indument is generally coarse, villi may become very slender and are responsible for the fine tomentose indu-ments of *B. croatii* and *B. broussonetiifolia*. Unless slides are prepared to determine the trichome type forming the tomentose indument, it is difficult to determine whether whiplash or villous trichomes are present. Villi occur on most plant parts, including internodes, petioles, inflorescences, stipules, bracts and sepals.

c. Scales.

Scales are flattened multiseriate trichomes consisting of cells of uniform size size and were first described in detail for *B. manicata* by Mayewski (1873) who termed them "barbules". They range in form from very narrow, entire scales through narrow lacerate scales to broad lacerate scales (Fig. 2E). In species with villous petiolar induments some very narrow, entire scales are often intermixed with the villi (e.g. *B. corredorana, B. morii).* Scales are most abundant on petioles, but may also be found on rhizomes, where they often form concentric bands around the petiole base, and on stipules, lower leaf surfaces and peduncles.

d. Whiplash Trichomes.

Whiplash trichomes are differentiated into a rounded basal section that is multiseriate or uniseriate and a long whiplash multiseriate to uniseriate distal portion consisting of elongate cells (Fig. 2H). Of the eight species with whiplash trichomes, only two, *B. conchifolia* and *B. pinetorum* have uniseriate basal sections. Although whiplash trichomes are usually slender and delicate, when they occur on rhizomes of certain species, they are more coarse with thicker basal portions and whiplike segments and are referred to here as coarse whiplash trichomes. In one species, *B. nelumbiifolia,* the trichomes are stiffened by sclerenchymatous cells from subepidermal layers (Fellerer, 1892), a condition which was first reported for villi of *B. imperialis* Lem. (sect. *Weilbachia* (Kl. & Oerst.) A.DC.) (Haberlandt, 1888). Trichomes of this species also occasionally appear to be glandular tipped apically. Whiplash trichomes are found primarily on petioles, leaf blades, stipules and inflorescences. These trichomes form the dense tomentose-lanate induments observed in *B. sericoneura* and several other species.

e. Barbate Trichomes.

These trichomes resemble whiplash trichomes in consisting of two cell regions, usually thick rounded or flattened basal portions but differ from whiplash trichomes in having two or more whiplike projections (Fig. 2G). On petioles of *B. cardiocarpa,* these trichomes often form narrow bands, frequently becoming connate basally and resemble scales, but differ from scales in their thickened basal portions and elongate cells distally. Barbate trichomes, however, are most often associated with rhizome internodes.

Leaves. *Begonia* leaves have two stipules which initially sheath immature leaves and the shoot apex. In sect. *Gireoudia,* stipules are deciduous to persistent, but in a few species they can be characterized as caducous or fugacious, depending on whether they fall before a new leaf begins expanding or as the leaf is maturing. They are slightly asymmetric and members of a stipule pair will be mirror images of each other (Fig. 3A). Unlike many other *Begonia* sections, stipules of species in sect. *Gireoudia* are well developed and vary in shape among the species, ranging in form from tri-

angular to ovate, oblong or lanceolate. For some species like *B. plebeja* stipule shape is a good diagnostic character. Stipules are usually strongly keeled, with the keel frequently becoming strongly lacerate or fimbriate, especially distally. In a stipule pair, the keel of one stipule is excurrent apically, while in the other, it is excurrent subapically. In general, only the outer member of a stipule pair has a lamina that is covered with an indument; while the lamina of the inner member is glabrous, the keel may be lacerate, fimbriate or pilose. Apically stipules are usually attentuate-acuminate and aristate or rarely acute to obtuse and aristate. Stipules of *B. quaternata* are unusual in being cucullate in the living state, but upon drying often split distally and appear obcordate. Since rhizomes are poorly collected in larger species, stipular information for these species is less than complete.

Phyllotaxy in sect. *Gireoudia* is alternate, with the two-ranked leaves borne on the same side of the stem or rhizome. The long, succulent petioles are typically terete or subterete, becoming weakly canaliculate basally, but, in one population of *B. heracleifolia (Utley & Utley 6983),* they were multicanaliculate throughout. They are usually strongly lenticellate, but this is frequently difficult to detect on dried herbarium material. Although the petiolar indument in a few species is variable (*B. heracleifolia, B. strigillosa*), in most species it is constant, but varies significantly among taxa, ranging from hirtellous or pilose to tomentose, lanate, villous or squamose and is often a good diagnostic character. Scales on petioles of *B. manicata* characteristically form one to several, dense concentric bands on the petioles just beneath the petiole-blade junction.

Leaf blades of most species are charta-ceous to coriaceous or infrequently succulent. In several rhizomatous species, ultimate leaves produced before the onset of the dry season are succulent, with thick hypodermal layers. These species include *B. conchifolia, B. cardiocarpa, B. heracleifolia, B. sericoneura* and *B. strigillosa*; of the mentioned species, only *B. conchifolia* typically has succulent leaves throughout the year. This behavior is maintained even when plants are cultivated under greenhouse conditions. Although a function of this condition is not known, it seems possible that these leaves could function as temporary water storage sites which could then be used to supply some of the plant's water requirements during the dry season. Leaves are persistent in the vast majority of taxa but are deciduous in several rhizomatous species with succulent rhizomes (e.g. *B. heracleifolia, B. plebeja*) which are adapted to seasonally very dry habitats. Under greenhouse conditions with plentiful water, the leaves continue to be deciduous and rhizomes will remain dormant for 2 to 3 months each year.

With the exception of mature specimens of *B. thiemei* with palmately compound leaves (Fig. 3B), leaves of Central American species in sect. *Gireoudia* are simple. Blades are medium to dark green on their adaxial surface, occasionally becoming red marginally, and are generally lighter beneath, but in *B. multinervia* the lower leaf surface is often deeply pigmented with anthocyanins and appears deep maroon. *Begonia strigillosa* from Mexico and Guatemala, and *B. plebeja* frequently have maculate leaves, with deep maroon or chocolate splotches throughout the lamina. While individuals with maculate leaves are striking and horticulturally desirable, maculation does not appear to be a useful taxo-

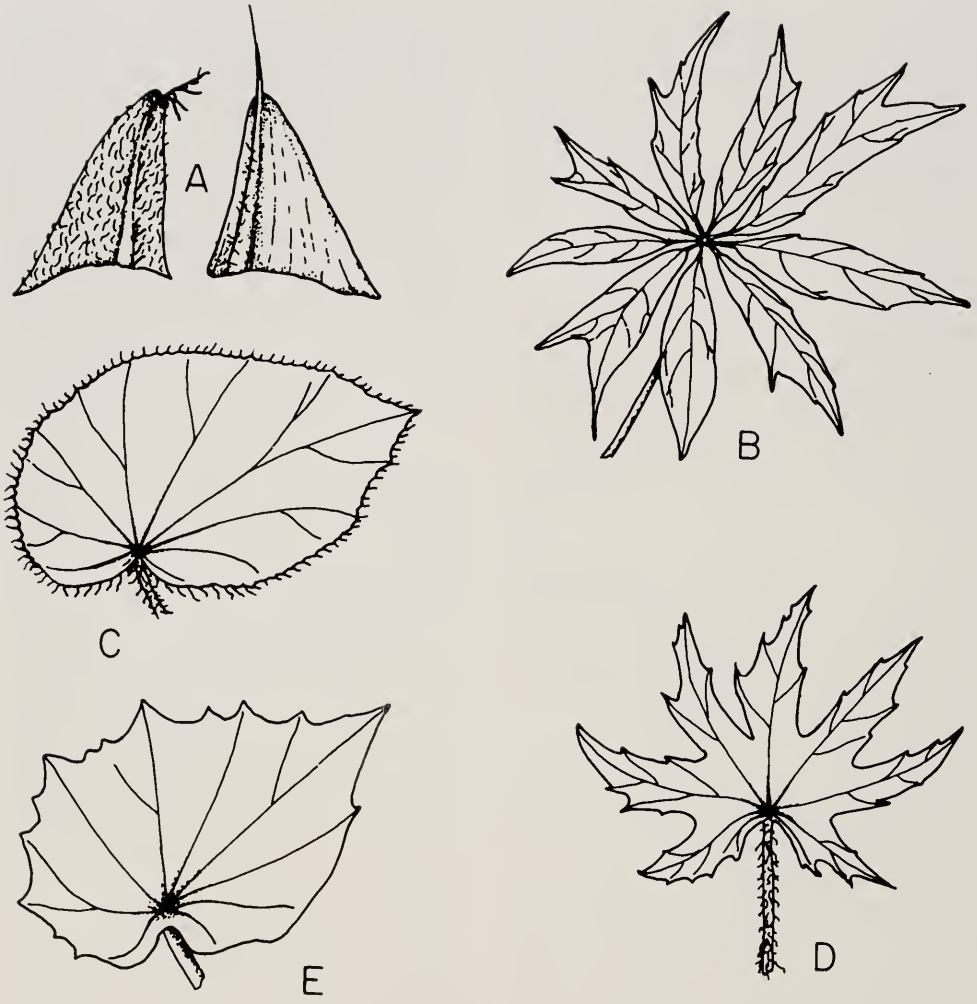

Fig. 3. Stipule and blade form in sect. *Gireoudia*. A. Stipules of *B. urophylla*. B. Palmately compound blade of *B. thiemei*. C. Oblique blade of *B. strigillosa*. D. Straight, palmately lobed blade of *B. heracleifolia*. E. Peltate blade of *B. fonsecae*. (A from *Utley & Utley 5708*; B from *Martínez-Calderón 2258*; C from *Utley & Utley 5772a*; D from *Breedlove 33963*; E from *Standley 29539*).

nomic character. Within populations of *B. strigillosa (Williams 26198)* and *B. plebeja*, individuals with maculate leaves grow intermixed with plants having plain leaves. The expression of maculation also appears to be influenced by environmental parameters (pers. obs.). Leaf blades of *B. heracleifolia* are often variously colored which has resulted in leaf color forms being recognized as distinct species (*B. punctata*) or varieties (*B. heracleifolia* var. *viridis*). Within a population of *B. heracleifolia* more than one color form can be observed. Like maculation, color development in these forms appears to be influenced by environmental conditions. The upper leaf surface varies from glabrous to hirtellous, pilose or hirsute or occasionally tomentose-lanate, but, unlike the lower leaf surface, is not typically squamose. Scales, if present, are restricted to principal

nerves proximally. In species with glabrous mature upper leaf surfaces, the leaves are often glandular when immature and unexpanded. The abaxial surface has an indument similar to that observed on the petioles, but in species with squamose petioles, the scales are restricted generally to the primary and secondary nerves.

Leaf morphology within sect. *Gireoudia* and *Begonia*, in general, is characterized by a pervasive asymmetry. Gentry (1969) considers leaf form the result of complex interactions among ecological parameters. Leaf blades in sect. *Gireoudia* are similar to those observed in most other *Begonia* sections and are obliquely to transversely inserted on the petioles (Fig. 3C) in all but four species in which the blade orientation is straight (Fig. 3D). In at least one of these species, *B. heracleifolia*, juvenile leaves are oblique. The transverse or oblique blade may be a compromise between efficiency and mechanical cost, minimizing the need for secondary supporting tissue while optimizing water and nutrient transport by approaching a radial transport system, which Givnish (1979) suggests is optimal but impractical for most plants. Leaf shape is variable within species and ranges from suborbicular through broadly elliptic or oblong to ovate or obovate. Great size differences can be observed among leaves on plants within a population and even on a single plant. As much as a five-fold variation in leaf size within a species can be observed. Some of variability results because individuals begin flowering their first year and generally will have smaller leaves than older, more established members of the population. *Begonia* leaves are also responsive to various environmental conditions which may influence leaf size, thickness and number (Dunn and Costa, 1972). *Begonia nelumbiifolia*, *B. fusca* and *B. thiemei* often have extremely large leaves, with the blades of *B. fusca* approaching 90 cm in length. Givnish (1979) believes large leaves are mechanically more economical than numerous smaller leaves which require a more elaborate support system and may be favored under certain conditions. As these species are rhizomatous, the support system is restricted to very succulent petioles with largely undifferentiated parenchyma and a modified stem. Because blades are often large, complete leaves of these three species are rarely collected or smaller often immature leaves are gathered instead. The morphometric measurements of blade and petiole size are a reflection of available collections and not necessarily an accurate measurement of size variation in these species.

Leaf apices are usually oblique and attenuate-acuminate in sect. *Gireoudia*, but rarely are acute to obtuse. *Begonia crassicaulis* and *B. heracleifolia* frequently lack a well-defined apical region because of their symmetric, lobed leaves. Basally cordate leaves are most common in sect. *Gireoudia* as in other *Begonia* sections, but several taxa have different leaf base forms. The change in leaf base form from cordate to rounded in *B. dressleri* and to cuneate in *B. buseyi* may have paralleled changes in leaf orientation from oblique or transverse to straight in both taxa. *Begonia fonsecae*, *B. conchifolia*, *B. nelumbiifolia* and *B. manicata* var. *peltata* bear basally leaves. Among this group *B. fonsecae* is anomalous with its peltate but pseudocordate leaves (Fig. 3E). This character combination has only been observed in sect. *Gireoudia* in an artificial hybrid (*Utley & Utley 5007a* X *Utley & Utley 4921*) and a putative natural hybrid between *B. conchifolia* and *B. sericoneura* (*Skutch 4600*). Smith (1979, pers. comm.) feels

that the peltate blade form is variable within individual plants and has observed single specimens with both peltate and non-peltate leaves. Within sect. *Gireoudia* this state has only been encountered in the previously mentioned hybrids. In artificial hybrids, leaves on a single plant may be cordate, peltate or pseudocordate and peltate, potentially resulting from developmental abnormalties in the hybrids. Wagner (1962) noted in a survey of irregular morphological leaf development in hybrid ferns that, if parents of a particular hybrid differed greatly in a particular character state, then that character might tend to develop irregularly in hybrid offspring. The peltate leaf form with its radial nerves should provide the most efficient arrangement of nerves for nutrient and water transport. Unlike many tropical groups that have largely entire leaf margins, leaf margins are rarely entire within *Begonia*. However, herbs and other understory plants in wet tropical forests often possess leaves with non-entire margins (Bailey and Sinnott, 1916). Reasons for differences in margination remain unclear but certainly can influence transpiration rates and convective heat loss (Givnish, 1979). Perhaps non-entire margins among Central American species in the section might function as multiple drip tips, facilitating leaf drying. Margination is usually ciliate and ciliate-denticulate or ciliate-serrulate and often dentate to doubly dentate or serrate to doubly serrate at ends of major nerves. Many taxa have a broad, but shallow apically rounded lobe on the side of the blade opposite the petiole insertion. Leaves of *B. urophylla* frequently have a secondary cusp or shallow lobe a few centimeters behind the apex, on the side opposite the base. Two species, *B. broussonetiifolia* and *B. involucrata*, have unusual bilobed or trilobed leaves. Leaf lobing is most pronounced in *B. heracleifolia* and *B. crassicaulis* with generally straight, palmately sinuate-lobed leaves. *Begonia sericoneura* and *B. manicata* exhibit clinal variation in leaf margination with leaves from the northern part of their range having cilate and ciliate-denticulate margins which are replaced by leaves with variously lobed margins further south. Reasons for these differences are unclear but may be a reflection of subtle habitat differences. Moreover, margination characteristic of adult leaves is not always observed in juvenile foliage (e.g. *B. heracleifolia*).

Leaf blades of almost all species in sect. *Gireoudia* are palmately nerved with 5-13 principal nerves but the four peltately-leaved taxa differ in having peltinerved blades. Following the classification of Hickey (1975), leaves of these species have actinodromous basal nerves and secondary venation patterns that are basically craspedodromous. The palmately compound leaves found in *B. thiemei* are an exception to this general pattern since the leaflets are pinnately veined and craspedodromous.

Inflorescences. Inflorescences of all species in sect. *Gireoudia* are borne laterally from axils of mature or immature leaves. Although they may occasionally appear dioecious because only staminate or pistillate flowers are evident, inflorescences within the section are uniformly monoecious. Inflorescences exhibit great infraspecific variation in size and the number of flowers they produce, which partially depends upon the size of the individual plant and microhabitat conditions, so that a large well-developed plant generally will produce inflorescences with larger peduncles and more numerous flowers than a smaller plant within the same population. In very large species, *B.*

fusca, B. nelumbiifolia and *B. thiemei,* the whole peduncle is rarely collected and occasionally only branches of the inflorescence will be gathered; thus, ranges of variation reported for inflorescence characters in these species were a reflection of available collections. It is likely these species occasionally have inflorescences much larger than have been collected. Like petioles, peduncles are very succulent and brittle with an indument which correlates well with that observed on the petioles but is frequently much less dense and, in some species, is wanting.

Irmscher (1914) presented a survey of inflorescence types found in *Begonia,* in which he recognized two basic inflorescence forms, cymes and racemes. An in depth survey of the inflorescence of *B. cucullata* Willd., a commonly cultivated species, was conducted by Matzke (1938) who showed that branches of initial dichasial cymes in *B. cucullata* became modified into cincinni. The Central American sections of *Begonia* contain species with predominantly cymose inflorescences, and the cyme or compound dichasium is characteristic of sect. *Gireoudia.* Although the suffrutescent species like *B. corredorana, B. multinervia,* and *B. sartorii* generally have symmetric inflorescences (Fig. 4A), the trend in the section is toward increasing cyme asymmetry. The majority of species bear dichasia that are moderately asymmetric (Fig. 4B) to strongly asymmetric or unilateral, resulting from a reduction of one of the two branches borne at each node (Fig. 4C). concomitant with a modification of the cyme in the ultimate and penultimate nodes, but occasionally in the node immediately preceding the penultimate node (the subpenultimate node). Inflorescence asymmetry has been used to distinguish among species (Smith and Schubert, 1958, 1961), but this character can be very unreliable unless infraspecific variability is well understood and is used in conjunction with other less equivocal characters. Inflorescence branching patterns have been modified in both *B. quaternata* and *B. involucrata. Begonia quaternata* produces modified symmetric cymes in which lower nodes are from two to six radiate, but almost 75% of the inflorescences examined possessed three to four radiate lower nodes (Fig. 4D). The number of branches per node vary among nodes within an inflorescence and between inflorescences on a single plant (*Utley 5688, Utley 5689).* Inflorescences of *B. involucrata* appear very dense because many, if not all, of their internodes are greatly reduced in length, so that many flowers appear to arise from a single node. A similar tendency has been observed in ultimate inflorescence internodes of some populations of *B. corredorana* in Costa Rica.

Generally, the central flower at each dichasial node is staminate, but in some species the central flower is missing at the first dichasial node. In several species cymes are largely symmetric throughout and ultimate nodes bear three flowers, a central staminate flower and two lateral pistillate flowers (Fig. 4E) or a lateral pistillate flower and lateral staminate flower (Fig. 4F). More often, the ultimate node, penultimate node and frequently subpenultimate node have modified branching patterns. Generally, several branching patterns are encountered in a single inflorescence, but without living material which can be observed regularly, differences in branching patterns may be difficult to determine from preserved specimens. In some inflorescences the subpenultimate node produces a normal branch and a central staminate flower, but then produces a

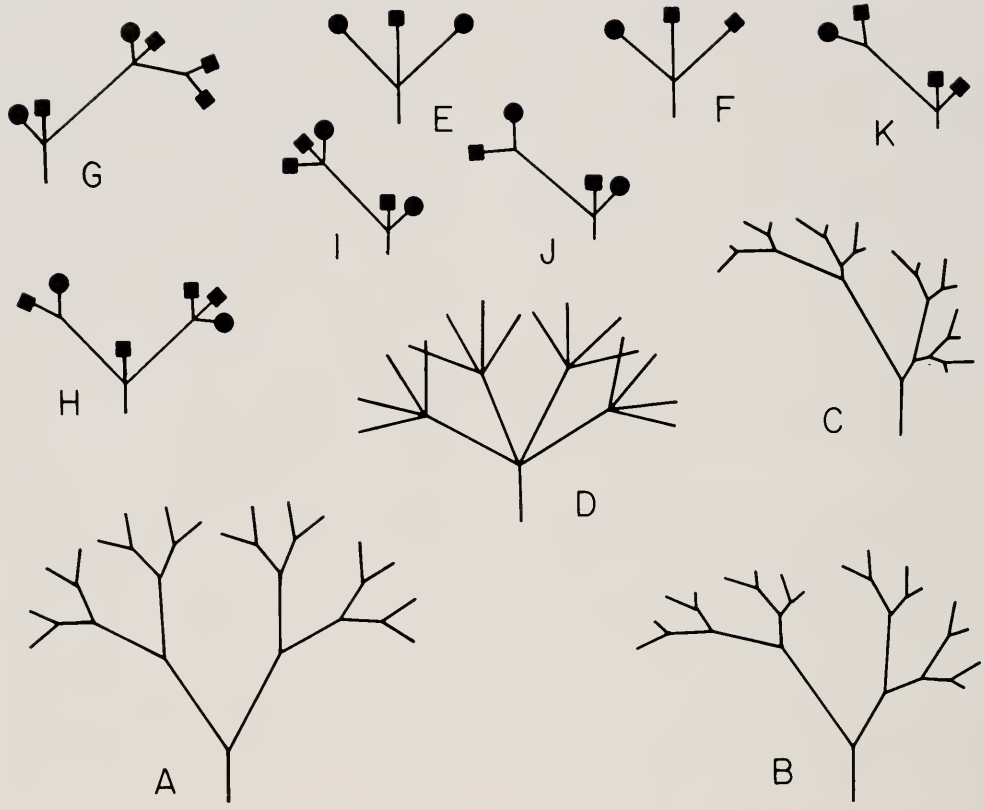

Fig. 4. Inflorescence form in sect. *Gireoudia*. A. Symmetric inflorescence. B. Moderately asymmetric inflorescence. C. Strongly asymmetric or unilateral inflorescence. D. Inflorescence four-radiate at lowermost nodes. E. Ultimate inflorescence node with a central staminate and two lateral pistillate flowers. F. Ultimate inflorescence node with central staminate flower and a lateral staminate flower and pistillate flower. G-K. Modified ultimate, penultimate and subpenultimate inflorescence nodes. Several branching patterns are often encountered within a single inflorescence. A ■ indicates a staminate flower; a ● indicates a pistillate flower.

pistillate flower in place of the second branch, while at the penultimate node both a staminate and pistillate flower are borne, along with a branch which then bears two staminate flowers (Fig. 4G). This sometimes is modified in such a way that the penultimate node produces one branch which bears two staminate flowers and a pistillate flower at the next node and a second branch that only has a pistillate flower and a staminate flower (Fig. 4H). More commonly, the penultimate node will produce a staminate flower, a pistillate flower and a branch which then develops one pistillate flower and two staminate flowers at the ultimate node (Fig. 4I) or, instead of three flowers, the ultimate node will only have a staminate and a pistillate flower (Fig. 4J). Sometimes the penultimate node has a second staminate flower instead of a branch while the branch bears a pistillate flower and a staminate flower (Fig. 4K).

Bracts. At each dichasial node in inflorescences of sect. *Gireoudia* are pairs of bracts that ensheath the young buds. The most frequently encountered arrangement of a bract pair is valvate, with the bract edges touching but not over-

lapping. In *B. broussonetiifolia* and *B. involucrata*, the bracts are modified into an outer and an inner bract, which results in the outer bract completely encircling the inner bract. In most species bracts are caducous to persistent, but in a few species they are fugacious, apparently abscising as soon as the peduncle begins elongating and remain either poorly known or unknown. Texture of bracts varies from membranaceous and translucent through chartaceous. Along with their unusual cochlear arrangement, bracts of *B. broussonetiifolia* and *B. involucrata* are very succulent, but when dry are most often chartaceous. Bracts decrease in size and change form from the lowermost node to the uppermost node, with the uppermost bracts greatly reduced in size. The lowermost pair of bracts is usually navicular and varies in morphology from oblong-elliptic through suborbicular to transversely elliptic or broadly obovate. Bracts are most often glabrous or grandular, but in a few species are pilose. The apices of bracts are most often obtuse or rarely acute or attenuate-acuminate. Marginally, bracts range from entire to ciliate-denticulate or ciliate-serrulate, but in *B. heracleifolia* they are unusual by being glandular-serrulate. Bracts are variable in color and are commonly green, pink or deep pink, with more intense coloration often developing in bracts on inflorescences in exposed locations.

Floral Morphology. Among Central American species in sect. *Gireoudia*, all but one, *B. pinetorum*, bear staminate and pistillate flowers in which it is possible to distinguish between sepals and petals. A perianth with two distinct whorls is not unique to the section, but rather is widespread among neotropical sections, occurring particularly in staminate flowers. Pistillate flowers in many sections, however, frequently have undifferentiated perianth parts. This was recognized by Candolle (1859; 1864) who referred to parts as sepals or petals in staminate flowers, but described pistillate flowers as being lobed. Neither Warburg (1894) nor Irmscher (1925) followed Candolle but rather standardized terminology by referring to perianth parts collectively as tepals. While Smith and Schubert (1946b) state they were able to recognize two distinct perianth series in staminate flowers, they followed Warburg and Irmscher in calling the parts tepals. However, in their characterization of the Begoniales, Smith and Schubert (1974) used sepals and petals to describe its perianth. Cronquist (1981) described staminate flowers as often having 2 unlike valvate sets of 2 tepals. In familial descriptions, some other authors (Benson, 1979; Lawrence, 1951) treat the Begoniaceae as having recognizable sepals and petals in staminate flowers but tepals in pistillate flowers, while Hutchinson (1959) used sepals and petals for Begoniaceae flowers in general.

Because of the importance of floral structure to an understanding of not only intrasectional relationships, but also intersectional relationships, it is imperative that a terminology allowing for the description of readily observable differences in perianth characters be utilized. Where outer and inner perianth whorls can be distinguished in staminate or pistillate flowers (e.g. *B. fusca*), I am calling the outer sepals and the inner petals. In species with only one whorl (e.g. *B. manicata*), with the exception of pistillate flowers of *B. pinetorum*, I refer to members of that whorl as sepals. In morphology this series appears identical to the outer series of previously mentioned flowers and is presumed to be homologous. *Begonia pinetorum* differs in producing pistillate flow-

ers with typically three to five relatively uniform perianth segments which are herein referred to as tepals.

a. Bracteoles

Staminate flowers within sect. *Gireoudia* are ebracteolate, and over half the species also produce ebracteolate pistillate flowers that lack all vestiges of bracteoles, a condition which appears widespread among Begonia species. Another group of species in sect. *Gireoudia*, characterized as having ebracteolate pistillate flowers, frequently will bear occasional pistillate flowers within an inflorescence that have rudimentary excrescences on their pedicels and infrequently minute linear or oblanceolate bracteoles. Subtending the pistillate flowers of four species (*B. crassicaulis, B. conchifolia, B. plebeja, B. sericoneura*) are pairs of well-developed, deciduous to subpersistent bracteoles (Fig. 5A). Bracteoles are usually borne at the base of the ovary, but may be several millimeters beneath the ovary on the pedicel as has been observed in some collections of *B. plebeja*. They are submembranaceous to membranaceous and in coloration, pubescence and margination are comparable to similar bract characters. Bracteoles vary in morphology from suborbicular to broadly obovate, transversely elliptic, elliptic, ovate or oblong. Little taxonomic significance is attached to variations in bracteole shape, but their presence or absence can be useful in distinguishing among morphologically otherwise similar taxa and in evaluating putative hybrids.

b. Sepals

Both staminate and pistillate flowers consist of two petaloid sepals with valvate aestivation which at anthesis are vertically oriented (Fig. 6A, 5B). In cultivation staminate flowers may persist almost a week after anthesis before abscising with their pedicels as a unit. In contrast, pistillate flowers will abscise if pollination has not occurred, but if it has, the sepals will eventually abscise. Sepals, which range in color from white to light or dark pink, depending upon the species, population and/or light exposure, vary from elliptic through suborbicular to elliptic, oblong, ovate, obovate, or occasionally in pistillate flowers, transversely elliptic or reniform. In any one species, sepals of several different shapes are commonly observed. With the exception of *B. fusca*, and at least some populations of *B. nelumbiifolia*, sepals are generally thin, with the result that their size and shape occasionally become distorted during specimen preparation. Another problem is the tendency for sepals in some species to change in shape slightly from suborbicular or ovate to oblong, obovate or elliptic at anthesis, making sepal shape a frequently unreliable character. Staminate and pistillate sepals may be approximately the same size or, in certain species (*B. urophylla*), the staminate sepals will be consistently larger than pistillate sepals. Morphometric differences among taxa, however, can be very significant since some species have very small sepals, while others have intermediate sized or large sepals. Externally sepals are either glabrous, glandular or sparsely pilose in sect. *Gireoudia*, with only a few species having occasionally or typically pilose sepals.

c. Petals

Petals are generally wanting in staminate and pistillate flowers, but several species occasionally have staminate flowers with one or two, obovate or oblanceolate petals that alternate with the sepals (Fig. 6B). In pistillate flowers, these

same species will frequently have pistillate flowers bearing usually a single petal which is oriented at a right angle to the sepals (Fig. 5C). Petals, when present, may abscise shortly after anthesis.

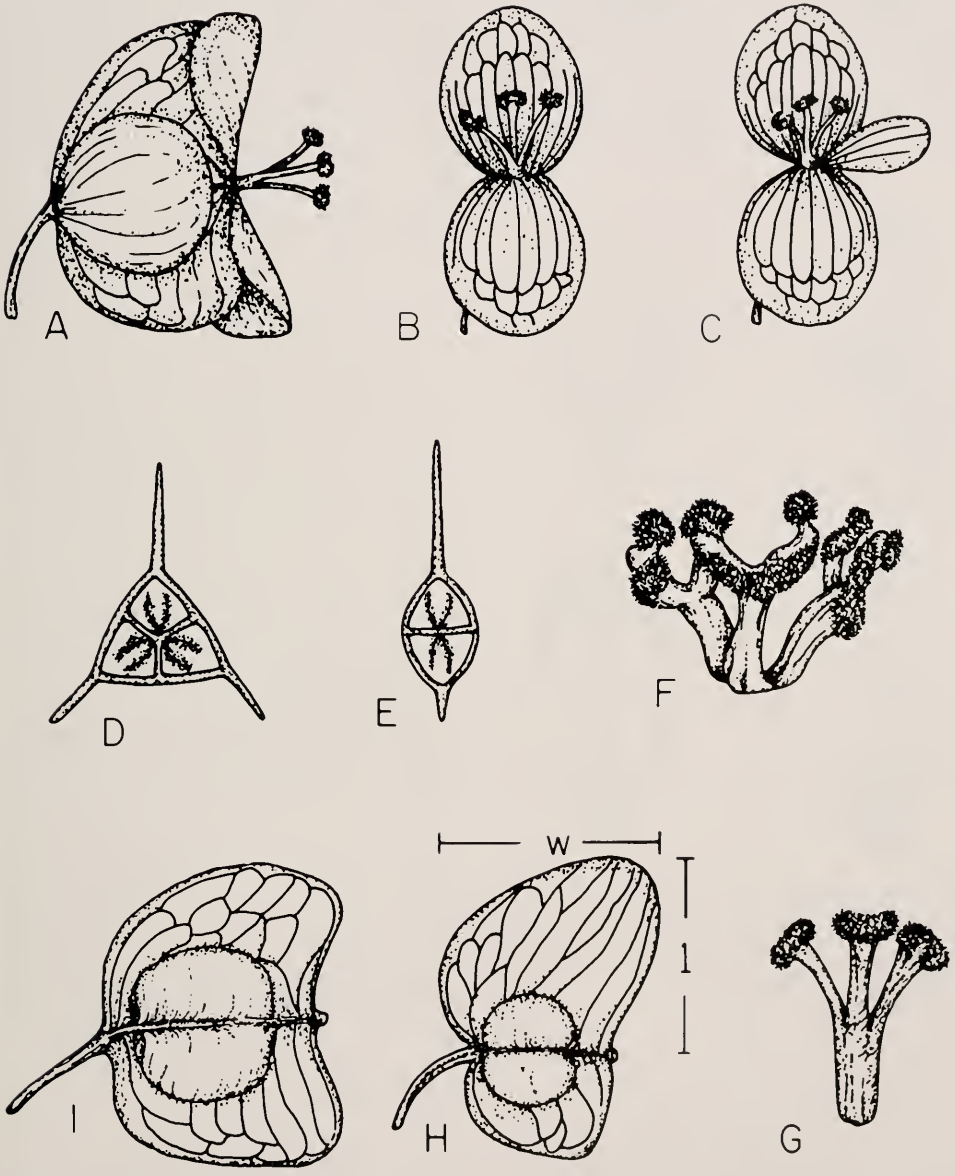

Fig. 5. Floral morphology of pistillate flowers in sect. *Gireoudia*. A. Profile of bracteolate pistillate flower. B. Pistillate flower with sepals. C. Pistillate flower with sepals and a petal. D. Cross-section of trilocular ovary showing bipartite placentae. E. Cross-section of bilocular ovary. F. Bicornute stigmas. G. Lunate stigmas. H. Capsule with unequal wings. I. Capsule with subequal wings. (A-D, G, I from *B. conchifolia, Utley & Utley 4458*; E from *B. dressleri, Dressler 4141*; F, H from *B multinervia, Utley 6015*).

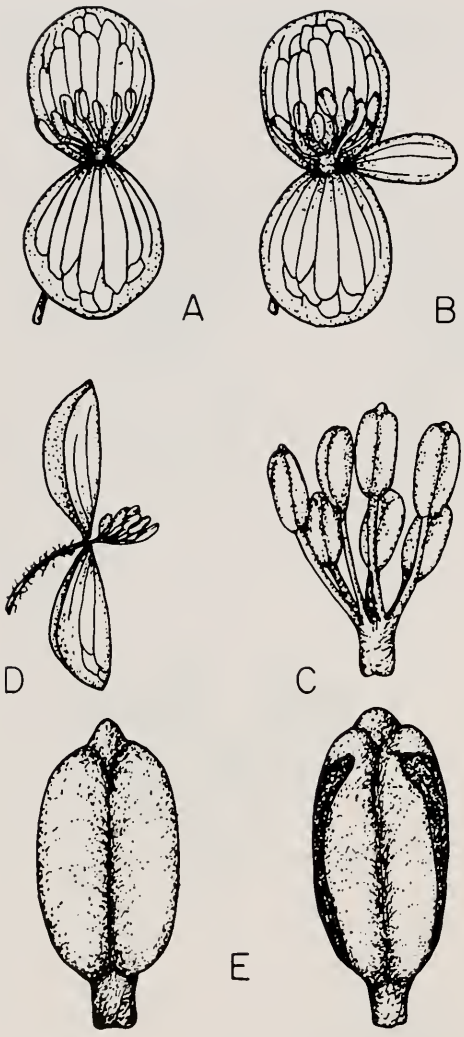

Fig. 6. Floral morphology of staminate flowers in sect. *Gireoudia*. A. Staminate flower with sepals. B. Staminate flower with sepals and petal. C. Stamens on raised receptacle. D. Profile of staminate flower. E. Anthers. (from *B. conchifolia, Utley & Utley 4458*).

d. Androecium

Stamens in sect. *Gireoudia* are fasciculate on a low or slightly raised subconvex torus or receptacle (Fig. 6C) and, at anthesis, their long axis is oriented perpendicular to the long axis of the sepals (Fig. 6D). Although stamen number has generally been imprecisely characterized as "stamens numerous" or "stamens few" and is of little value as such, once infraspecific variation has been determined, stamen number has significant taxonomic value in sect. *Gireoudia* because it varies widely among species, with some species having as few as 5 stamens (e.g. *B. manicata*) while others have up to 82 stamens (e.g. *B. fusca*). The filaments are short but of varying lengths within a fascicle, and may be free or weakly connate basally. Alphonse de Candolle (1864) described such filaments in sect. *Gireoudia* as submonadelphous and, in *B. quaternata*, the filaments often appear strongly submonadelphous or even monadelphous. Anthers are similar in form among the species and are oblong, oblong-elliptic or obovate, but vary in size from 0.6-3.1 mm long and are two-thecate (Fig. 4E). Pollen is shed at anthesis through arcuate longitudinal fissures.

Pollen grains of species in sect. *Gireoudia* are typical of many other *Begonia* taxa in being 3-colporate and prolate-perprolate with striate exines. Among the Central American members of the section, pollen is uniformly small, ranging between 17.5-22.5 X 11-17.5 μ. Although it was reported that grains of one species (*B. heracleifolia*) were almost twice the size of another (*B. nelumbiifolia*) (Hoover, 1979), such size variation was not observed in the present study. Tetrads also have been reported in *Begonia* (Erdtman, 1966), but none were seen among the species examined.

e. Gynoecium

The inferior ovary characteristic of *Begonia* is three-locular with axial placentation and bipartite placentae in sect. *Gireoudia* (Fig. 5D). Although placentae are two-lobed, there is a tendency for lobes to become unequal in

some species, like *B. cardiocarpa*. In *B. fusca* and *B. garagarana* placentae differ from the placentae usually observed in sect. *Gireoudia* by being strongly vertically sinuate-ridged. Placentae, in general, are described as being "ovuliferous throughout" because numerous anatropous ovules are attached to both internal and external placental surfaces. The bilocular ovaries observed on some specimens of *B. dressleri* represent an unusual modification of the three-locular ovary in which the two locules are vertically situated (Fig. 5E). This arrangement of locules differs from that found in the bilocular species in sect. *Weilbachia* and is also anomalous within *Begonia*. Externally, ovaries are glabrous, sparingly glandular or occasionally pilose, but never squamose.

The styles, calyx and corolla, when present, arise from the summit of the ovary. *Begonia* species have from two to five distinct or basally connate styles (Hutchinson, 1959, Lawrence, 1951), but within sect. *Gireoudia* pistillate flowers have three styles that range from being weakly connate basally to connate two-thirds their length. *Begonia dressleri* is an exception, having two or three styles depending upon the pistillate flower examined. Among Neotropical *Begonia* sections, the bicornute stigma form predominates and lunate stigmas are only infrequently encountered. However, in sect. *Gireoudia* less than 50% of the species studied from Central America had bicornute stigmas (Fig. 5F) while the majority had lunate stigmas that ranged from broadly to narrowly lunate (Fig. 5G). This suggests that, at least within sect. *Gireoudia*, lunate stigmas are a derived condition. Only six rhizomatous species occurring in Central America (*B. croatii, B. fusca, B. garagarana, B. louis-williamsii, B. nelumbiifolia* and *B. urophylla*) are characterized by bicornute stigmas, while the remaining 15 species have lunate stigmas. Bicornute stigmas predominate among the suffrutescent taxa, with only *B. sartorii* having lunate stigmas. Differences in stigma form are very useful in distinguishing among morphologically otherwise similar taxa and were largely responsible for a re-evaluation of *B. stigmosa* and the recognition of *B. urophylla*. The stigmatic surface in both stigma types consists of a single, densely papillaceous band that extends the length of the stigma.

Capsules. The fruit of sect. *Gireoudia* and most other begonias is a bony, loculicidal capsule that dehisces basally along slits on each side of the wings (Fig. 5H). Even after capsules shed their seeds, they remain attached to the senescing inflorescence. Total capsule length, from base to apex, or locule length varied greatly among the species and can be useful in distinguishing between species. The external shape of locules varies within species and, therefore, appears to be of minimal taxonomic significance. In the species examined the shape ranged from oblong to elliptic, suborbicular, ovate, or transversely elliptic. The relationship of capsule wings to one another can be characterized as equal to subequal in which all wings are well-developed and the same size or roughly similar in size (Fig. 5I) or unequal, in which case one wing is significantly larger than the other two (Fig. 5H). In some species with unequal wings, a large dorsal or primary wing is present but the lateral wings are greatly reduced and may appear marginiform, while in others the dorsal wing is large, but the lateral wings are well-developed. This latter condition is potentially intermediate between capsules with subequal wings and those with unequal wings with largely marginiform secondary wings. Since

lateral wings were frequently marginiform, only dorsal wings were consistently measured. Wing length was determined by measuring the distance from a capsule's central axis to the wing tip; width was measured at the widest point above the locule chamber (Fig. 5H). Within a species and frequently within a single inflorescence several different dorsal wing shapes exist, but they are generally asymmetric with oblique apices. In shape dorsal wings are usually broadly triangular to ovate, oblong-elliptic or dolabriform. Lateral wings are most often broadly asymmetrically triangular, lunate-triangular, lunate or marginiform.

Seeds. Seed coat morphology of *Begonia* sect. *Squamibegonia* Warb. was studied with SEM by Bouman and De Lange (1982) who recently surveyed seed coat structure of a number of *Begonia* species representing several sections (Bouman and De Lange, 1983). Seitner (1972) also examined *Begonia* seeds, describing ranges in seed size and variations in seed coat patterns, but the value of this latter study is diminished by an apparent lack of voucher specimens. The numerous seeds borne in capsules of species in sect. *Gireoudia* are small, 0.2-0.55 mm long, and oblong, oblong-elliptic or occasionally obovate in shape, becoming constricted proximally (Fig. 7A). The testa is reticulate and light brown at maturity (Fig. 7A, B). The seeds contain straight, oily embryos and no endosperm.

Breeding System and Hybridization

Species within sect. *Gireoudia* are monoecious and produce both pistillate and staminate flowers within the same inflorescence. While this prevents autogamy, it does not necessarily increase xenogamy (outcrossing) unless geitonogamy (crossing among flowers within an inflorescence) is minimized, since *Begonia* is self-compatible (East, 1940). Many monoecious taxa are temporally dioecious, bearing pistillate and staminate flowers at different times (Cruden and Hermann-Parker, 1977). A number of species in sect. *Gireoudia* including *B. urophylla* and *B. multinervia* appear to be temporally dioecious, producing staminate flowers first and then pistillate flowers which do not reach anthesis until most staminate flowers have abscised. A large number of species, such as *B. sericoneura, B. plebeja* and *B. quaternata*, are temporally dioecious but toward the end of the pistillate phase will produce some staminate flowers so that limited geitonogamy can occur. Most begonias have several inflorescences, and in species which tend toward temporal dioecism, flowering is synchronized so that there is little to no overlap between pistillate and staminate phases among inflorescences. Examples of this condition are *B. involucrata* and *B. multinervia*. Although *B. conchifolia* and *B. strigillosa* are initially protandrous, pistillate flowers quickly reach anthesis and there is no further temporal separation between phases which should maximize geitonogamy in these species. This may be important in species that often occur in small isolated populations, because it would permit pollination in the absence of other individuals with staminate flowers at anthesis simultaneously.

Pistillate flowers of *Begonia* offer no obvious rewards to pollinators (Vogel, 1978); staminate flowers offer only pollen and neither staminate nor pistillate flowers observed in sect. *Gireoudia* have a detectable odor, but fragrance may be associated with flowers of some other *Begonia* taxa (Seitner, 1976). It is now generally recognized that pistillate flowers of *Begonia* mimic the staminate

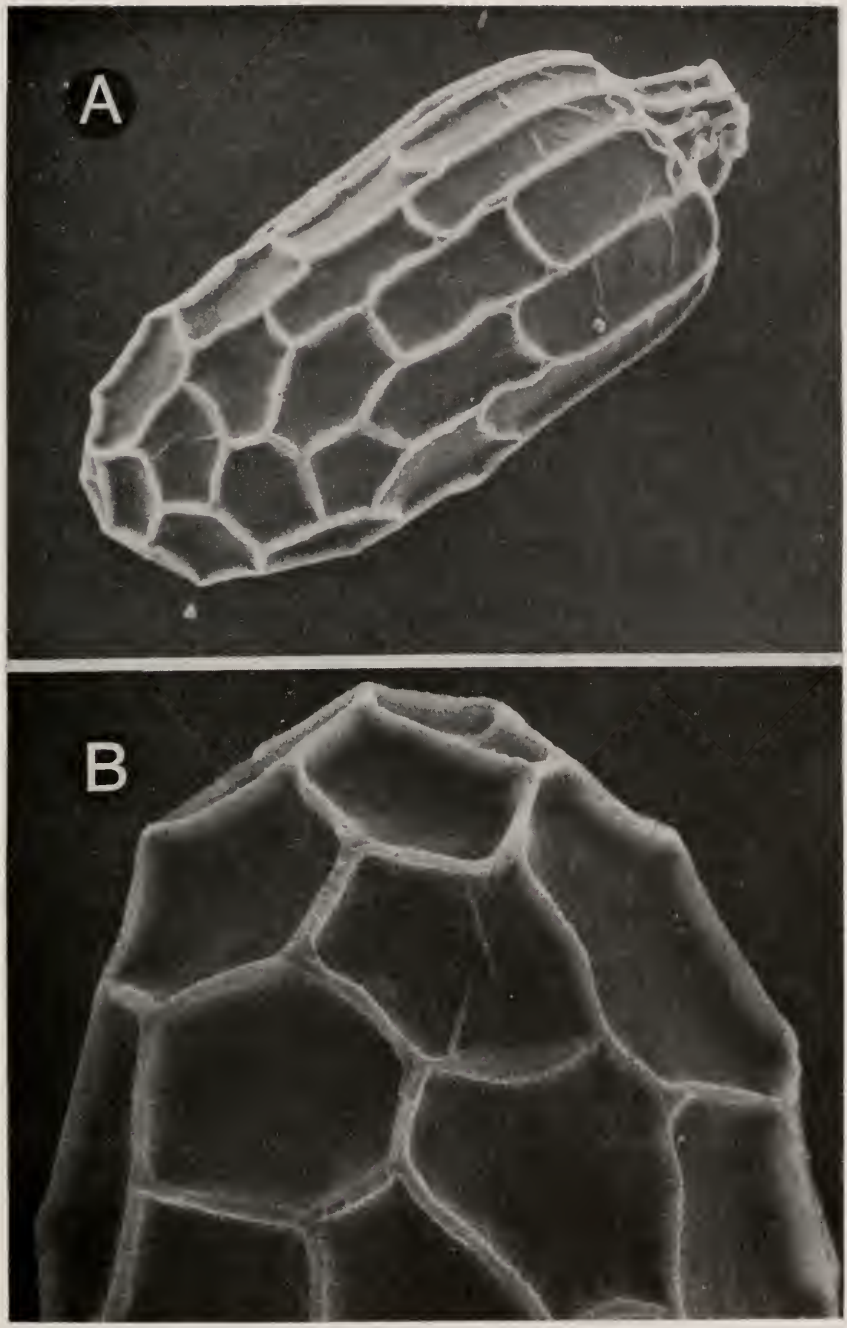

Fig. 7. Seed coat morphology of *Begonia sericoneura*. A. Seed. X200. B. Close-up of seed coat. X500. (from *Utley & Utley 4623*).

flowers (Pijl, 1978; Vogel, 1978; Wiens, 1978; Givnish, 1980). In their yellow coloration and general conformation, the stigmas look like the androecium and may deceive pollinators into visiting them, resulting in "mistake" pollination. In *Carica* where "mistake" pollination was first reported, pollinators visit pistillate flowers only briefly before leaving and searching for more staminate flowers (Baker, 1976). Floral mimicry and resulting mistake pollination have been demonstrated recently in another genus in the Caricaceae (*Jacaratia*) (Bawa, 1980) and may be important in other groups as well (Bawa, 1977; Givnish, 1980). Syrphidae (Seitner, 1976) and bees (Seitner, 1976; Wiens, 1978; Givnish, 1980) have been reported visiting *Begonia* flowers largely in cultivation, but I have never observed bees or other potential pollinators visiting *Begonia* flowers in the field in Mexico or southern Central America.

In sect. *Gireoudia,* flowers of different taxa strongly resemble one another in form, coloration and posture at anthesis, so that there appear to be no strong morphological barriers to interspecific pollination. The major differences among the staminate flowers of species involve stamen number and size of morphological parts. Subtle distinctions may also exist in inflorescence symmetry, cyme density and number of flowers per inflorescence which may be significant in preventing interspecific pollination as was noted by Bell (1971) for Umbelliferae. Positive assortative pollination (Levin, 1970) could also reduce the potential for hybridization, if species growing sympatrically were of differing heights.

Natural hybridization has not been widely recognized among *Begonia* species although begonias readily form artificial, frequently fertile hybrids in cultivation. While hybridization is not rampant in sect. *Gireoudia,* it appears to occur often when two species are sympatric, but does not usually result in large hybrid swarms. A primary factor that may diminish the effects of interspecific pollination is the generally low level of seedling establishment observed in many *Begonia* populations. One described taxon in sect. *Gireoudia, B. barsalouxii* Standl., is thought to be of hybrid origin and a second, *B. fonsecae* is suspect because of its unusual shriveled anthers which produce no viable pollen. Hybridization involving the following species has been observed in this study: *B. sericoneura* x *B. conchifolia, B. sericoneura* x *B. corredorana, B. sericoneura* x *B. urophylla* and *B. heracleifolia* x *B. nelumbiifolia.*

Skutch 4600 from Pejivalle, Costa Rica involves four specimens at GH, MO, NY and US. One collection (MO) consists of an element strongly resembling *B. conchifolia* in its small, peltate leaves and few stamens (8-10) but was unusual in its often deformed anthers. Two other collections of *Skutch 4600* (NY, US) resemble *B. sericoneura* in their thick rhizomes and basally cordate leaves, but their leaf blades are smaller than those generally observed on *B. sericoneura* (6.5-10.2 vs. 7-22 cm long). The leaves of these specimens are also unusual in that they are ciliate-denticulate but not dentate or serrate to irregularly lobed like most specimens of *B. sericoneura* from Costa Rica. In this respect their margins are similar to *B. conchifolia* margins which are usually denticulate-serrulate or somewhat crenulate. With respect to their inflorescences, young inflorescences have both pistillate and staminate flowers at anthesis simultaneously. Although this is atypical of *B. sericoneura,* it is common in *B. conchifolia* inflorescences. Both sepals (5.5-6 vs. (6)8-14 mm long) and ovaries (6.5-

8.5 mm vs. 7-10 mm long) are slightly smaller than those observed on most specimens of *B. sericoneura*. Stamen number in these specimens also is lower than usually observed in *B. sericoneura* (20-24 vs. 35-61) and slightly higher than *B. conchifolia* which has 6-13 stamens. The fourth specimen at GH was anomalous with its basally peltate, but strongly pseudocordate leaves, while other characters resembled the material at NY and US. Pollen from all four specimens was sampled and stained with cotton blue-lactophenol to gain further evidence for their hybrid origin. Collections of *B. conchifolia* and *B. sericoneura* were also sampled to determine their pollen viability. These data are summarized in Table 1. Although the putative hybrids produced about 40% non-viable pollen as indicated by non-staining grains, they also produced significant levels of apparently viable pollen. An artificial hybrid between *B. conchifolia (Utley & Utley 5077a)* and *B. sericoneura (Utley & Utley 4921)* has recently been synthesized in this study. These hybrids exhibit a range of leaf base forms from cordate through peltate and pseudocordate. In leaf margination and floral morphology they also resemble the putative natural hybrids. While pollen viability was reduced in the putative natural hybrids, the potential for introgression with one or both parents would exist, as long as the hybrids produced some viable pollen.

Intrasectional Relationships

In his treatment of *Gireoudia*, Klotzsch (1855) divided the species he included into two groups based upon stem orientation. The first group consisted of suffrutescent species and species with potentially erect rhizomes, while those with repent rhizomes were placed in a second group. Beyond this organization Klotzsch made no attempt to discuss potential species affinities or similarities.

TABLE 1. Morphological comparison of *B. conchifolia*, *B. sericoneura* and their putative natural hybrid.

	B. conchifolia	Intermediate *Skutch 4600*	*B. sericoneura*
Leaf blade size (cm)	2-9(14) X 1-8(10)	6.5-10.2 X 4.1-7	(4) 7-14(22) X (4) 6-12(16)
Leaf base	peltate	peltate, cordate or peltate and pseudocordate	cordate
Margination	denticulate-serrulate, undulate	ciliate-denticulate	dentate or serrate to doubly dentate, irregularly lobed
Sepal size (mm)	4-8(13) X 4-8(10.5)	5.5-6 X 4.5-7	(6)8-14 X 8-14(16)
Stamen number	6-13	18-24	(14)28-61
Ovary length (mm)	4-6.5	4.5-6.5	(4)7-10
Pollen viability	*Utley 5881* 1-95% 2-95% 3-100%	*Skutch 4600* (GH)—60% (NY)—58% (US)—58%	*Utley & Utley 3921* 1-97% 2-98% *Utley & Utley 4623* 98%

When Candolle (1864) treated sect. *Gireoudia* in his monograph of the Begoniaceae, he recognized three subsections within sect. *Gireoudia* which he circumscribed primarily on differences in leaf form. The only species then known with palmately compound leaves, *B. carolineifolia* from Mexico, Candolle placed in its own intrasectional taxon, while both species with palmately lobed leaves, *B. crassicaulis* and *B. heracleifolia,* constituted the second subsection. The remaining 30 species were grouped in a subsection that Candolle characterized as having variously lobed, dentate or peltate leaves. Within this taxon Candolle organized species into two groups, those with occasional staminate petals and those without staminate petals. Of the three species which Candolle included in the group with occasional petals, only one, *B. sericoneura,* is presently included in sect. *Gireoudia.* Personally, I have not observed staminate flowers with petals in this species, although pistillate flowers occasionally bearing ephemeral petals have been observed. Although *B. lindleyana* has been excluded from sect. *Gireoudia,* its sectional relationships remain in doubt (see Doubtful and Excluded Species). Most taxa which Candolle considered to have apetalous staminate flowers represent a diversity of growth forms and a number of species in this group are now known to have staminate flowers with petals infrequently. Warburg (1894) recognized three subsections within sect. *Gireoudia* (as sect. *Magnusia),* depending upon the number of pistillate "tepals." The majority of taxa were included in subsection *Gireoudia* which was characterized by pistillate flowers with two sepals or tepals. Emphasizing the distinctness of *B. pinetorum,* Warburg placed it in its own subsection, *Psathurou,* which differed from other subsections by its pistillate flowers with four tepals. The remaining subsection, *Rachia,* consisted of a single species, *B. incana* Lindl., that could be distinguished by its pistillate flowers with three tepals and is presently referred to sect. *Knesebeckia.* In his treatment of the Begoniaceae for Die Natürlichen Pflanzenfamilien, Irmscher (1925) concurred with Warburg in his treatment of sect. *Gireoudia* and most other sections. Neither treatment, however, provided insight into species similarities or affinities, except in the very broadest context. As with Candolle's monograph, the majority of species were included in a single infrasectional taxon. Since Irmscher's treatment, species within sect. *Gireoudia* have been studied in the context of floristic surveys and there has been little attempt to address potential species affinities or, for many taxa, even to indicate sectional alliances (Smith and Schubert, 1958, 1961).

Species within sect. *Gireoudia* have been here tentatively organized into species groups based upon phenetic similarities among the species (Table 2), but these groupings do not constitute a formal recognition of intrasectional taxa. A number of Central American species show no close affinities to other Central American species and have been placed in their own species groups. Because insufficient information concerning endemic Mexican taxa was available during the course of this study, no attempt was made to include them in the species groups presented.

The characteristics utilized to divide taxa into species groups include plant habit, trichome form, stipule form, stigma type, bracteole presence and capsule wing form. Three of the five suffrutescent species constitute the multinervia species group which, with the exception of *B. sartorii* from Mexico and

TABLE 2. Species groups of Central American *Begonia* section *Gireoudia*.

1. dressleri species group—*B. buseyi, B. dressleri*
2. fonsecae species group—*B. fonsecae*
3. fusca species group—*B. fusca, B. garagarana*
4. heracleifolia species group—*B. heracleifolia*
5. involucrata species group—*B. broussonetiifolia, B. involucrata*
6. manicata species group—*B. cardiocarpa, B. manicata*
7. multinervia species group—*B. corredorana, B. multinveria, B. sartorii*
8. nelumbiifolia species group—*B. nelumbiifolia*
9. pinetorum species group—*B. pinetorum*
10. sericoneura species group—*B. conchifolia, B. crassicaulis, B. plebeja, B. sericoneura*
11. strigillosa species group—*B. louis-williamsii, B. morii, B. strigillosa*
12. thiemei species group—*B. thiemei*
13. urophylla species group—*B. croatii, B. quaternata, B. urophylla*

Guatemala, is centered in Costa Rica. Along with their suffrutescent habit these species have generally symmetric inflorescences and ebracteolate pistillate flowers. The two taxa from southern Central America, *B. corredorana* and *B. multinervia* also share their villous trichomes and bicornute stigmas, while *B. sartorii* differs from the group in its whiplash trichomes and lunate stigmas. The remaining suffrutescent taxa, *B. broussonetiifolia* and *B. involucrata* form the involucrata species group which is potentially closely allied to the multinervia species group with which it shares a similar habit, floral and capsular characters and distribution in southern Central America. The involucrata species group is distinguished primarily by its strongly lobed leaves, unusual bracts and often tomentose indument formed from slender villi or whiplash trichomes.

The urophylla species group encompasses those taxa which have squamose or villous-squamose induments or rarely villous induments, repent rhizomes often similar leaf blades, ebracteolate pistillate flowers and usually narrowly ovate to oblong or dolabriform primary capsule wings and includes three Central American species. Two of the species, *B. croatii* and *B. urophylla,* have bicornute stigmas, while the third, *B. quaternata,* is characterized by broadly lunate stigmas. Although *B. croatii* and *B. quaternata* are very narrow endemics known from only a few localities, the remaining species in the group, *B. urophylla,* is widely distributed in Central America. Such broad distributional patterns have been observed in only three other species groups. With similar rhizomes, stipules and squamose, villous-squamose or villous induments, species in the strigillosa species group resemble the urophylla species group. They, however, stand apart in their generally much smaller leaf blades, often lunate stigmas and broad primary capsule wings. Among the group, only *B. louis-williamsii* has bicornute stigmas. Aside from *B. strigillosa,* which has a range of induments from squamose, through villous-squamose and villous, indument form is constant within the species. *Begonia strigillosa* also differs from the other members in its subequal capsule wings and broad distribution.

Like the urophylla and strigillosa species groups, the sericoneura species group consists of species with rhizomatous habit. Members of this group share their induments of whiplash trichomes, lunate stigmas, bracteolate pistillate flowers, broadly ovate to triangular capsule wings and well-developed secondary capsule wings. In two of the four species

rhizome orientation is characteristically erect or ascending. The fonsecae species group, consisting of only *B. fonsecae,* a poorly known species from Honduras, is closely allied with the sericoneura species group, differing primarily in its ebracteolate pistillate flowers. The pinetorum species group is also similar to the sericoneura species group in its succulent rhizomes and whiplash trichomes, but it is distinguished from this group and other species by its pistillate flowers which regularly have three to four undifferentiated tepals.

In their succulent ascending rhizomes, members of the manicata species group strongly resemble species within the sericoneura group. With this group they also share their lunate stigmas, but differ primarily in their indument which is squamose in *B. manicata* but villous in *B. cardiocarpa* and is comprised of scales or a mixture of coarse whiplash trichomes and barbate trichomes. This group differs from the urophylla species group primarily in its succulent, erect rhizomes and equal to subequal capsule wings. Closely allied with both the manicata and sericoneura species groups is the heracleifolia species group. The relationships among these groups are discussed in greater detail in the discussions of individual species.

The remaining four species groups encompass taxa with rhizomatous habits that have no clear association with other species groups. They differ from one another in leaf blade orientation and form, indument, stigma form and primary capsular wing form. A discussion of the relationships of species in these groups to other taxa is presented in the discussion of each species.

Taxonomic Treatment

Begonia sect. *Gireoudia* (Kl.) A.DC., Ann. Sci. Nat. IV. 11: 133. 1859.

Gireoudia Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854. Lectotype: *B. plebeja* Liebm.

Magnusia Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854. 125. 1854. TYPE: *Magnusia maxima* Kl.

Begonia sect. *Psathuron* A.DC., Ann. Sci. Nat. IV. 11: 131. 1859. TYPE: *B. pinetorum* A.DC.

Begonia sect. *Magnusia* (Kl.) A.DC., Prodr. 15(1): 333. 1864.

Begonia sect. *Aurifornia* Ziesenhenne, The Begonian 41: 13. 1974. TYPE: *B. bakeri* C.DC.

Erect suffrutescent herbs, or acaulescent to caulescent rhizomatous herbs, with erect or repent, often succulent rhizomes; internodes very short to much elongate, glabrous to variously pubescent. Leaves alternate, two ranked, blades simple or rarely palmately compound, persistent or deciduous, membranaceous to coriaceous or succulent, oblique to transverse, rarely straight, basally cordate or infrequently peltate or rounded to cuneate, marginally highly variable, palminerved or peltinerved, with 4-13 primary nerves, glabrous or variously pubescent. Stipules fugacious to persistent. Inflorescences axillary, cymose, generally 2-radiate at each node but occasionally 2-6 radiate, internodes elongate, rarely reduced or aborted, symmetric to asymmetric or unilateral, few- to many-flowered. Bracts 2 at each inflorescence node, fugacious to subpersistent. Staminate flowers: with two valvate sepals, only infrequently one or two petals present; stamens few to numerous, 5-82, fasciculate on a low torus, filaments free to submonadelphous or monadelphous, anthers oblong, elliptic or obovate, dehiscing through arcuate longitudinal fissures. Pistillate flowers: usually ebracteolate, but occasionally bracteolate with two bracteoles at the ovary base or infre-

quently on the pedicels; sepals two, valvate, only infrequently a petal present or rarely with 3-4 undifferentiated tepals; ovary inferior, styles 3 or rarely 2, connate basally to two-thirds their length. Capsules loculicidal, locules dehiscing basally on both sides of wings, trilocular or rarely bilocular with bipartite placentae, ovuliferous on all sides, with 3 or rarely 2 wings, wings unequal or occasionally subequal to equal, dorsal or primary wing variable in form, lateral wings well-developed or marginiform; seeds minute, 0.2-0.5 mm long, testa reticulate.

DISTRIBUTION: Central Mexico through Central America to Colombia and Venezuela in northern South America.

I have selected *B. plebeja* as the lectotype of *Gireoudia* because it agrees well with the protologue of *Gireoudia* and is one of the more commonly collected and widely distributed species, ranging from Mexico to Panama. Although Baranov and Barkley (1979) designated lectotypes for the sections of *Begonia* including *Gireoudia*, they arbitrarily chose the first species listed by an author in a section or genus (e.g. A.DC., 1859; as per Klotzsch, 1855 not the original publication of Klotzsch's genera, 1854) and without regard for the protologue. Because of these factors, their designations of lectotypes contravene Article 8 of the International Code of Botanical Nomenclature.

Explanation of Key

Characters important in distinguishing the species in *Begonia* sect. *Gireoudia* have been described in the section on morphology. Several traits which are very useful in species determinations within the section are plant growth form, petiolar and internodal indument, stigma shape, stamen number and the capsule wing relationship. Identification of certain taxa can be difficult unless complete floral material is available because vegetatively many species are morphologically similar or are variable in leaf form and size. With most herbarium material it is possible to quickly discern if a specimen is suffrutescent or rhizomatous because suffrutscent taxa have generally longer internodes that rarely have roots while the majority of the rhizomatous taxa have shorter internodes with numerous roots, and specimens of these species are frequently accompanied by quantities of soil and detritus. Two rhizomatous taxa, *B. cardiocarpa* and *B. manicata*, which have erect rhizomes, may consequently be mistaken for suffrutescent species on occasion, but generally they can be distinguished from suffrutescent taxa by their shorter, thicker internodes and their internodal indument. Measurements for all morphological characters were taken from dried herbarium material, and for floral measurements in particular, it is important to use only dried material as floral parts often shrink upon drying. Where a taxon is variable in a particular character state, it will key out more than once. While the key is artificial and is not meant to indicate relationships among taxa, morphologically similar species are frequently nearest neighbors in the key.

Key to the Central American Studies of Begonia Sect. Gireoudia

1. Leaves peltinerved or palmately compound.
   2. Leaves compound; Mexico to Honduras ..... 15. *B. thiemei*
   2. Leaves simple
      3. Petioles squamose, consisting of lacerate scales; Guatemala ..... 16. *B. manicata* var. *peltata*
      3. Petioles hirsute, tomentose-lanate or pilose with fine or coarse whiplash trichomes.
         4. Leaf blades large, 15-40 X 11-32 cm; petioles hirsute; Mexico to northern South America ..... 14. *B. nelumbiifolia*
         4. Leaf blades usually small, 2-15.5 X 1-11 cm; petioles tomentose-lanate, at least when immature but often becoming pilose with age.
            5. Leaf blades 2-9(14) X 1-8(10) cm; staminate sepals 3.5-6.5 X 2.8-6.5 mm; stamens 6-13; pistillate flowers bracteolate; ovaries 4-6.5 mm long; wings on ovaries or capsules subequal; Costa Rica-Panama ..... 23. *B. conchifolia*
            5. Leaf blades 13.5-15.5 X 8.5-11 cm; staminate sepals 6.5-7 X 6.5-7 mm; stamens 27-30; pistillate flowers ebracteolate; ovaries 7-10 mm long; wings on ovaries or capsules unequal; Honduras ..... 22. *B. fonsecae*

1. Leaves palmately nerved, simple.
   6. Leaf blades straight, or occasionally the apex slightly oblique.
      7. Leaf blades basally cordate, deeply palmately lobed.
         8. Petioles squamose, villous-squamose or villous; rhizomes repent; bracts subpersistent, marginally glandular-serrulate; Mexico-Honduras (Panama) ..... 18. *B. heracleifolia*
         8. Petioles tomentose-lanate, with fine whiplash trichomes; rhizomes erect or ascending; bracts caducous, marginally ciliate-denticulate to serrulate; Mexico-Guatemala ..... 19. *B. crassicaulis*
      7. Leaf blades basally rounded to cuneate, leaves unlobed or with a broad but shallow lobe, never palmately lobed.
         9. Leaf blades narrowly elliptic, obovate or rhomboid; upper leaf surfaces glabrous; leaf bases cuneate; stamens 11-13(19); ovaries 2-3 mm long; capsules 3-4.5 mm long, three-locular with three wings; Panama ..... 26. *B. buseyi*
         9. Leaf blades suborbicular or broadly obovate; upper leaf surfaces hirtellous or glandular-hirtellous; stamens 7-10(13); ovaries 3-4.5 mm long; cap-

sules 4-5 mm long, three-locular or rarely two-locular, generally with three wings, but if two-locular, then with two wings; Panama .... 25. *B. dressleri*

6. Leaf blades oblique to transverse.

10. Inflorescence nodes with 3-5(6) branches, only rarely 2-branched at lowermost nodes; stipules caducous, but if present cucullate or split apically and appearing obcordate; stamens with filaments submonadelphous to monadelphous; Costa Rica-Panama ..... 10. *B. quaternata*

10. Inflorescence internodes 2-branched at lowermost nodes, only rarely 3-branched; stipules caducous to persistent, not cucullate, apically attenuate-acuminate, acuminate or rarely acute; stamens with filaments borne on a low or raised torus, occasionally submonadelphous.

11. Petiolar indument squamose or villous-squamose; rhizomatous herbs.

12. Leaves glabrous above to sparsely glandular or if hirsute, then leaves palmately lobed; stigmas lunate.

13. Leaves palmately lobed ..... 18. *B. heracleifolia*

13. Leaves unlobed or only with a broad cusp or lobe on the side of the leaf opposite the petiole insertion.

14. Internodes generally very short, 0.2-0.8 cm long; rhizomes 2-11 (39) cm long, repent; internodes sparsely to moderately squamose; inflorescences few-flowered; staminate sepals 6-10 X 5.5-10 mm; Southern Mexico to Panama .... 11. *B. strigillosa*

14. Internodes 1.1-3.5 cm long; rhizomes 4-200 cm long, erect or ascending; internodes glabrous or rarely sparsely squamose or glandular; inflorescences generally many-flowered; staminate sepals 2.5-6.5(8) X 2-5(7.5) mm; Mexico-Nicaragua ..... 16. *B. manicata*

12. Leaves hirsute above, only rarely glabrous, occasionally with a broad lobe or cusp on the side of the leaf opposite the petiole insertion, never palmately lobed; stigmas bicornute.

15. Stamens 16-18; leaf blades 8.7-13 X 3.5-5.7 cm; inflorescences few-flowered; peduncles 6.5-17.5 cm long; ovaries 7-9 mm long, capsules unknown; Guatemala ..... 12. *B. louis-williamsii*

15. Stamens (23)33-61; leaf blades (8.1)10.4-29.3 X (4.3)6-16.5(19.7) cm; inflorescences generally many-flowered; peduncles (8)(24-80 cm long; ovaries (3.5)4-6.4 mm long; capsules (6)7-10 mm long; Guatemala to northern South America ..... 8. *B. urophylla*

11. Petiolar indument villous, tomentose-lanate, hirsute or pilose, never squamose or villous-squamose; suffrutescent or rhizomatous herbs.

16. Leaves glabrous above.

17. Leaves palmately lobed ..... 18. *B. heracleifolia*
17. Leaves unlobed or with a broad lobe or cusp on the side of the leaf opposite the petiole insertion; if bi- or trilobed, then stems upright.
    18. Capsule and ovary wings subequal.
        19. Rhizomes generally repent, internodes generally short, 0.2-0.8 cm long, squamose; inflorescences usually few-flowered; staminate sepals 6-10 X 5.5-10 mm; stamens 6-17; pistillate flowers ebracteolate ..... 11. *B. strigillosa*
        19. Rhizomes generally erect or ascending; internodes 0.5-2.3 cm long, coarsely villous with whiplash and barbate trichomes; inflorescences usually many-flowered; staminate sepals 4-9 X 3.5-9 mm; stamens (12)16-32(37); pistillate flowers with small bracteoles; Honduras-Costa Rica ..... 17. *B. cardiocarpa*
    18. Capsule and ovary wings unequal.
        20. Stems upright; inflorescences symmetric to weakly asymmetric; suffrutescent herbs.
            21. Leaves strongly distally bi- or tri-lobed, the sinus 1/3 to 2/3 the width of the blade; Costa Rica .... 4. *B. broussonetiifolia*
            21. Leaves unlobed or with a broad but shallow lobe opposite the petiole insertion.
                22. Petioles and internodes densely lanate, becoming pilose with age with an indument of whiplash trichomes; stamens 11-19; stigmas lunate; Mexico-Guatemala ..... 2. *B. sartorii*
                22. Petioles and internodes villous; stamens 16-27; stigmas bicornute; Nicaragua, Costa Rica and Panama ..... 1. *B. multinervia*
        20. Stems repent; inflorescences generally asymmetric to unilateral; rhizomatous herbs.
            23. Internodes generally elongate, 0.9-5.5 cm long, puberulous when young; stipules caducous, oblong to lanceolate, 1.7-3.4 X 0.5-0.9 cm; staminate sepals 0.9-1.5 X 0.8-1.6 cm; stamens 30-46; pistillate and staminate flowers frequently with petals; stigmas bicornute; capsules 4-8 mm long; dorsal capsule wing dolabriform, ovate or elliptic, (1.4)2-2.8 X (0.7)1.1-1.5 cm; lateral wings marginiform; placentae strongly vertically ridged; Panama .... 6. *B. garagarana*
            23. Internodes generally short, 0.2-1 (1.2) cm long;

villous to squamose; stipules persistent, triangular, (0.4)0.9-1.6 (2) X 0.4-1.4 cm; staminate sepals 0.4-1.3 X 0.4-1.1 cm; stamens 11-28; petals rarely present (*B. plebeja*); stigmas lunate; capsules 9-15 mm long; dorsal capsule wing ovate to asymmetrically triangular, rarely oblong, 0.8-1.6 X 0.8-1.7 cm; lateral wings well-developed; placentae unridged.

24. Petioles pilose or glabrate with whiplash trichomes; internodes 0.8-1.8 (2.5) cm diam. with an indument of coarse whiplash or barbate trichomes; pistillate flowers bracteolate; Mexico to Panama ..... 21. *B. plebeja*

24. Petioles villous; internodes 0.4-1.1 cm diam.; villous to squamose; pistillate flowers ebracteolate; Panama ..... 13. *B. morii*

16. Leaves pilose to hirsute above.

25. Capsules or ovaries with subequal wings; pistillate flowers with 3-4 tepals; Mexico-Guatemala ..... 24. *B. pinetorum*

25. Capsules or ovaries with unequal wings; pistillate flowers with 2 sepals and occasionally 1 petal.

26. Pistillate flowers bracteolate; petiolar indument of fine whiplash trichomes; stigmas lunate.

27. Rhizomes generally erect to ascending, often silver-gray; petioles densely lanate on new growth; stipules ovate, broadly lanceolate or triangular; stamens (14) 28-61; Mexico to northern South America ..... 20. *B. sericoneura*

27. Rhizomes repent, brown; petioles sparsely pilose or glabrate; stipules triangular; stamens 11-24; Mexico-Panama ..... 21. *B. plebeja*

26. Pistillate flowers ebracteolate; petiolar indument of villi; stigmas bicornute.

28. Stems upright, internodes (0.6)0.9-10 cm long and usually less than 1 cm diam.; suffrutescent herbs.

29. Leaf blades essentially unlobed or with a broad but shallow lobe opposite the petiole insertion; Costa Rica- Panama ..... 31. *B. corredorana*

29. Leaf blades generally strongly lobed with one or more pronounced secondary lobes.

30. Leaf blades marginally ciliate and ciliate-denticulate; stipules caducous or infrequently deciduous; internodes 0.6-1.2 cm diam.; inflorescence internodes greatly reduced or aborted; pedicels of pistillate flowers (0.6)1.6-2.5(3) cm long, extending to (1.5) 2.1-3.6 (6) cm in fruit; Costa Rica-Panama ..... 5. *B. involucrata*

30. Leaf blades only rarely ciliate or denticulate except at apices of major lobes; internodes 0.2-0.6 cm diam.; stipules persistent; inflorescence internodes elongate; pedicels of pistillate flowers 0.6-0.9 (1.4) cm long, extending to 1.1-1.8 (2.1) cm in fruit; Costa Rica ..... 4. *B. broussonetiifolia*

28. Stems repent, internodes usually 0.5-3 cm long, but if longer, then usually more than 1 cm diam.

31. Petioles tomentose-lanate; staminate sepals membranaceous, 3-4 X 3.5-4.5 mm; staminate petals wanting; stamens 11-22; capsules 4.5-6.5 mm long; wings marginally entire; Panama ..... 9. *B. croatii*

31. Petioles hirsute; staminate sepals subcoriaceous, 10-20 mm X 10-19 mm; petals often present; stamens 50-82; capsules 9-15 (19) mm long; wings often marginally ciliate; Mexico, Guatemala and Honduras ..... 7. *B. fusca*

1. *Begonia multinervia* Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 18. 1852. TYPE: COSTA RICA: In monte Jaris, 3000 ft, November 1846, *Oersted s.n.* (Lectotype: C!; isolectotypes: B!, C! [2 sheets]).

Gireoudia multinervia (Liebm.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

Begonia glandulosa sensu A.DC., Prodr. 15(1): 339. 1854. non *B. glandulosa* Hook.

Begonia cuspidata C. DC., Bull. Bot. Soc. Belg. 45: 260. 1896. TYPE: COSTA RICA: Bords du Río Platanar près Buenos Aires, February 1892, *Tonduz 6524* (Lectotype: G!; isolectotypes: BR! [2 sheets], G!, US!)

Suffrutescent herbs; *stems* ascendant or occasionally sprawling, generally unbranched, 1-3 m tall; internodes elongate, (0.5) 1-7 X 0.2-1.3 cm, hirsute with rufous to ferrugineous antrorse trichomes 0.4-2 (5) mm long, frequently with minute glandular trichomes interspersed. *Leaf blades* simple, chartaceous, oblique to transverse, asymmetrically ovate to oblong-elliptic, 7-25 (29.1) X 3-15 (18.5) cm, basally broadly but shallowly cordate, infrequently deeply and narrowly cordate with lobes overlapping, apically attenuate-acuminate to abruptly short acuminate, marginally entire to undulate or irregularly serrulate-denticulate, rarely cuspidate at ends of major

nerves, occasionally with a very broad but shallow apically rounded lobe opposite the petiole insertion, upper surface dark green and nitidous, glabrous, glandular or rarely sparsely hirtellous, lower surface deep maroon or rarely light green and glabrous throughout or sparsely pilose on principal nerves only, 8-12-palmatinerved. *Petioles* maroon to light green, 4-16 (21) cm X 1-3 (4) mm, sparsely villous with antrorsely spreading villi (0.3) 0.5-2.5 mm long, occasionally with minute glandular trichomes interspersed, glabrescent with age. *Stipules* persistent to subpersistent, light green drying to cinnamon-ferrugineous, membranaceous, ascending but spreading to strongly reflexed with age, asymmetric, narrowly ovate-triangular to lanceolate, 1.7-3.7 (5) X 0.8-1.9 (2.1) cm, strongly keeled with the costa excurrent apically to subapically, marginally revolute and entire, glabrous. *Inflorescences* generally exceeding the foliage, regularly cymose, few- to many-flowered, 7.5-32 (36) cm diam. *Peduncles* (7) 11-31 (39) cm X 1-9 mm, glabrous to sparsely pilose but glabrescent with age. *Bracts* caducous, light green to pink, the lowermost navicular, ovate, elliptic or suborbicular, 0.7-2.1 X 0.6-1.7 cm, weakly keeled, apically acute, marginally entire. *Staminate flowers*: pedicals 4-10 mm long; sepals externally white to pale or deep pink, suborbicular to broadly elliptic, ovate or occasionally broadly transversely elliptic, 4.5-9 X 5-10 mm, glabrous; petals wanting; stamens 17-35 (47); filaments 0.3-1.8 mm long, inserted on a low torus; anthers narrowly oblong-elliptic or obovate, 1-2 X 0.3-0.9 mm. *Pistillate flowers*: pedicels 4.5-15 mm long; bracteoles wanting or obsolete; sepals colored like staminate sepals, suborbicular, broadly elliptic or transversely elliptic, (2.5) 4-8 X 3-9 mm, glabrous; petals wanting; ovary 3.5-8 mm long; styles 3, 1.2-1.8 mm long, connate to 1/2 their length, stigmas bicornute. *Capsules* with pedicels 5-25 mm long, trilocular, 6-9 (14) mm long; locule chambers externally suborbicular, broadly oblong-elliptic or weakly ovate, 4-8 (10.5) X 4-7.5 (8.5) mm; wings unequal, the largest asymmetrically ovate, triangular, oblong-elliptic or infrequently dolabriform, 8-18 X 6.5-13 (17) mm, apically obtuse, the second symmetric, broadly lunate to triangular, 3.5-7 (11) X 4.5-10 (12) mm, the third marginiform or shallowly lunate.

DISTRIBUTION AND HABITAT: Nicaragua to western Panama from sea level to 1100 m. *Begonia multinervia* is an aggressive colonizer, forming large populations along roadsides, streambanks and exposed, moist rocky banks in tropical and premontane wet regions in Costa Rica. Although most abundant in these ruderal habitats, *B. multinervia* also forms small populations in dense primary forests. It is one of few Costa Rican species growing on the calcareous soil characteristic of the Fila Cal in SE Costa Rica (Fig. 9).

FLOWERING: Peak period from November through March and then sporadically through July.

DISCUSSION: *Begonia multinervia* is one of the most widespread and abundant *Begonia* species in Costa Rica, but is infrequently reported from adjacent Panama and has just recently been collected in Nicaragua (*Vincelli 200*). The lack of collections from both these countries may be partially a reflection of the inaccessibility of much of the Caribbean watershed in these countries. In these areas it is also likely that suitable weedy habitats are not available or have not been available for sufficient periods to enable *B. multinervia* to establish the dense colonies observed in Costa Rica.

Begonia multinervia is one of several suffrutescent species in sect. *Gireoudia* from Central America. It is recognized by its habit, lanceolate, strongly keeled stipules, waxy unlobed leaves that are frequently deep maroon beneath and regularly cymose inflorescences. The major variations observed in *B. multinervia* involve size, stem orientation and bracteoles. Stems of individuals from forested habitats are frequently sprawling, whereas stems of their counterparts from exposed habitats are erect or ascending. Although leaf blades are very variable in size, they are uniform in other characters including the ratio of length to width, shape, margination, pubescence and coloration. Similar size variation is observed in other morphological characters. Pistillate flowers of *B. multinervia* are characteristically ebracteolate, but individual pistillate flowers have been observed which possess one or two minute bracteoles, minute swellings or excrescences on their pedicels.

I have selected a lectotype for *B. multinervia* from one of the three sheets at Copenhagen, and a specimen of *Tonduz 6524* at Geneva as a lectotype for *B. cuspidata* from the many collections which Candolle cited in his original publication of this latter taxon. *Begonia cuspidata* was previously treated as a synonym of *B. multinervia* (Smith and Schubert, 1958) and in salient features agrees with *B. multinervia*.

Included in *B. multinervia* is *B. glandulosa* sensu A.DC. (1864), but not *B. glandulosa* Hook. Alphonse de Candolle (1859) identified *Seemann 1662* from San Lorenzo, Veraguas as *B. glandulosa,* considering it to be the same taxon as *Hoffman 14* which Klotzsch had previously annotated as *Wageneria glandulosa* Kl. an epithet he never published and Candolle (1864) unequivocally rejected. Hooker (1861) published *B. glandulosa,* citing both Candolle's annotation of the Seemann collection and material he received under the name *B. nigro-venia* from Linden. Recognizing that *Seemann 1662* was the same species as *B. multinervia,* Hooker placed *B. multinervia* in synonymy with *B. glandulosa.* His illustration, plate 5256, and description concur with each other, but differ significantly from *B. multinervia* in both their rhizomatous habit and pistillate flowers with 4 tepals and lunate stigmas. Because of this, *Begonia glandulosa* Hook. was recently lectotypified by plate 5256 (Burt-Utley, 1984). In the Prodromus, Candolle (1864) included *B. glandulosa,* and it is clear from his descriptions of habit and pistillate flowers that he based his concept of this taxon upon both *Seemann 1662* and the Hoffman collection at Berlin. He, however, cited plate 5256 in his description and followed Hooker in also including *B. nigro-venia* Hort. Linden in *B. glandulosa,* but made no mention of *B. multinervia* which he treated as a distinct species. Based both on his description and the specimens he included, *B. glandulosa* sensu A.DC. is clearly conspecific with *B. multinervia.*

Begonia multinervia is most closely allied with two other suffrutescent species in sect. *Gireoudia, B. sartorii* and *B. corredorana.* Relationships within the multinervia species group are discussed under *B. corredorana* and *B. sartorii* and are summarized in Table 3. *Begonia multinervia* is readily differentiated from the remaining suffrutescent taxa in Central America, *B. involucrata* and *B. broussonetiifolia,* by its unlobed leaves which are frequently deeply pigmented with anthocyanins beneath and its generally valvate floral bracts. Both *B. broussonetiifolia* and *B. involucrata* have strongly sinuate-lobed leaves which are unpig-

TABLE 3. Morphological comparison of *Begonia corredorana*, *B. multinervia* and *B. sartorii*.

	B. corredorana	*B. multinervia*	*B. sartorii*
Upper leaf surface	hirsute	glabrous	glabrous
Leaf size (cm)	(13.5)16-28.2 X (7.4)9-15.5(19)	7-25(29) X 3-15(18.5)	12-20(23.9) X 8-16.8
Leaf margination	ciliate-denticulate, ciliate	entire to undulate or irregularly denticulate	ciliate-denticulate, ciliate
Petiole length (cm)	7-10	4-16(21)	5.2-13(22)
Petiolar indument	villous	villous	lanate when immature
Trichome type	coarse villi	coarse villi	whiplash trichomes
Inflorescence internodes	ultimate sometimes aborted	elongate	elongate
Stamens	16-41	17-35(47)	11-19
Pistillate pedicals (mm)	5-12(20)	4.5-15	6-10(18)
Stigmas	bicornute	bicornute	lunate

mented and unusual bracts in which the outer encircles the inner. Since *B. multinervia*'s inflorescence branches are never aborted or reduced, it can be immediately separated from *B. involucrata* which has reduced inflorescence internodes. These taxa also differ in the length of their pistillate pedicels. Unlike *B. broussonetiifolia* and many populations of *B. involucrata* which have tomentose petiolar induments, those of *B. multinervia* are villous.

SPECIMENS EXAMINED: NICARAGUA. Zelaya: 6.3 km S of bridge at Colonia Yolania, 200-300 m, *Vincelli 220* (MO). COSTA RICA: Alajuela: Cuesta de la Vieja, 750 m, *Biolley 958* (BR); La Vieja, *Biolley 1000* (BR); Surubres près San Mateo, *Biolley 7048* (BR, CR, G, US); *Biolley 17403* (B, US); Collines au Piedades près San Ramón, 1025 m, *Brenes 5485* (CR, F, NY); *Brenes 5487* (CR, F); "Alto de la Calera" de San Ramón, *Brenes 5878* (CR); camino de Santiago y La Calera de San Ramón, *Brenes 6479* (CR); Río Jesús de San Ramón, *Brenes 15003* (CR, F); Alrededores de San Ramón, *Brenes 15097* (CR, F); San Pedro de San Ramón (Catarata), *Brenes 21436* (F); below Cataratas de San Ramón, *Croat 46812* (MO); Río San Rafael, Hacienda la Marina, 14 km NE of Villa Quesada, 500 m, *Molina et al. 17413* (F); *Molina et al. 17447* (F); *Molina et al. 17450* (F): Caribbean watershed, Villa Quesada, 850 m, *Smith H1633* (F); Caribbean rain forest, Sucre, Canton San Carlos, 1000 m, *Smith F1850* (F); Los Angeles de San Ramón, 1100 m, *Solis Rojas 496* (F, MO); Río Naranjo, 200 m, *Tonduz 7607* (BR, CR, G); hillsides above Río Sarapiquí along rd to Colonia Virgen del Socorro, 700-800 m, *Utley & Utley 4690* (DUKE); road banks and disturbed primary forest 4-5 km N of Bijagua, 500-600 m, *Utley 5928* (DUKE, F); about 13.5 mi E of Arenal and 6.5 mi W of Fortuna, *Wilbur & Stone 10267* (DUKE); slopes of Volcán Santa María near rd from Liberia to Colonia Blanca, *Wilbur 25100* (DUKE); Atlantic rain forest area on Hacienda La Marina, Río San Rafael, 450-500 m, *Williams et al. 29112* (F). Cartago: rd from Río Pacuare to Grano de Oro, 600-1200 m, *Croat 36554* (MO); rd from Turrialba to Moravia, 2500 ft, *Foster 2722* (GH, US); steep forested slopes of Río Reventazón valley on grounds of ICA, 600 m, *Maas 898* (CR); *Schubert & Rogerson 614* (US); *Schubert & Rogerson 858* (MICH, US); Río Turrialba, 500 m, *Smith 6510* (B, GH, BM, M, US); Atirro, 500 m, *Smith 6511* (US); Pejivalle, 900 m, *Standley & Valerio 46885* (US); forêts de Tuis, *Tonduz 10149* (US); Río de las Vueltas, Tucurrique, *Tonduz 13010* (B, BM, F, GH, LE, M, P, US); rocky river banks 2-3 km of La Suiza, 700 m, *Utley 6003* (DUKE, F, GH, MO, NY, US); moist road banks 9.0-12.5 km E of Tuis, 800-900 m, *Utley 6015* (BR, CAS, CR, DUKE, F, G, GH, MEXU, MICH, MO, US); mountains above Río Pacuare, about 15 km W of Moravia, 800 m, *Williams 19495* (US); Río

Pejibaye near Atirro, 650 m, *Williams 19596* (US). Heredia: Río Puerto Viejo, La Selva, OTS Field Station, *Grayum 2636* (DUKE); La Selva, *Hammel 7890* (DUKE); valley of Río Sarapiquí, just above San Rafael, *Moore 6579* (BH, US); Río Puerto Viejo, Puerto Viejo de Sarapiquí, *Schubert & Holdridge 1358* (A, US). Limón: between Limón and Siquirres nearer to Siquirres, Río Madre de Dios, *Burger 10520* (F); semi-open banks of Río Toro Amarillo, Guapiles, 350 m, *Godfrey 66342* (MO); just E of Río Pacuarito, 5 km E of Siquirres, *Utley 6066* (CR, DUKE, F, GH, MO, US). Puntarenas: Esquinas forest, between Río Esquinas and Palmar Sur de Osa, *Allen 5776* (F); 1-2 km N of Dominical along road banks bordering river, *Almeda & Nakai 4127* (CAS); 9 km N of Villa Neilly, rd to San Vito, 3000 ft, *Almeda, Nakai & Verity 4294* (CAS); orillas del mar de Golfito de Osa (Golfo Dulce), *Brenes 12295* (CR, F); above Río Terraba about 10 km ENE of Palmar Norte, 40 m, *Burger & Matta 4652* (BM, CR, MO, NY, US); 5 km W of Rincón de Osa, Osa Peninsula, 50-200 m, *Burger & Liesner 7295* (CR, F); forest along Río Barú near Dominical, 0-20 m, *Burger, Visconti & Gentry 10662* (F, MO); undisturbed forest, Quebrada Palito, Burica Peninsula, 20-270 m, *Croat 22606* (MO, NY, USF); W facing slopes 5 km N of Villa Neilly, 1500 ft, *Gillis & Plowman 10070* (F); Río Volcán, 48 km SE of San Isidro, 330 m, *Jiménez 3753* (F); *Molina et al. 18155* (F); mangrove swamp and adjacent slopes, Rincón de Osa, *Liesner 1906* (MO); ridge trail from Palmar Norte to El Cedral y Maiz, 640-740 m, *Moore 6554* (BH, US); Terraba, 260 m, *Pittier 3909* (BR, CR, G); forêt à Boruca, *Tonduz 4144* (BR); Río Platanar près Buenos Aires, *Tonduz 6524* (M); Río Ceibo près Buenos Aires, *Tonduz 6568* (BR); 8-10 km N of Villa Neilly in Fila Cal, 900 m, *Utley & Utley 4849* (CR, DUKE, F, MO); 2 km N of Dominical along CR 223, 40 m, *Utley & Utley 4936* (CR, DUKE, MO); E of Buenos Aires along rd to Puente, 300-400 m, *Utley 5949* (CR, DUKE, F, MEXU, US); 1-2 km E of Dominical, 4 m, *Utley 5978* (B, C, CAS, CR, DUKE, G, GH, K, MO, NY, TEX, US); 14 km SE of Buenos Aires, Carretera Interamericana, *Wilbur 20917* (DUKE); 5 km NE of Buenos Aires and 2 km E of Salitre, 550 m, *Wilbur 25308* (DUKE); Maxwell Cone's "El Volcán" farm at jct of Río Angel and Río Volcán, 450-500 m, *Williams, Jiménez & Williams 24224* (F, US); wet rocky banks in rain forest area along Río Sonador, near Panamerican Hwy, El General Valley, 600 m, *Williams 28768* (F). San José: above Río Chirripó del Pacífico, between Canáan and Chimirol, 1000 m, *Burger & Liesner 7107* (F, MO, NY, US); 4.5 mi SW of Canáan, 900 m, *Croat 43435* (MO); Candelaria *Hoffmann 14* (B); steep banks of Río Pejibaye, vicinity of San Isidro, 340 m, *Molina et al. 18214* (F); El General, *Pittier 10622* (BR, CR, US); *Skutch 2146* (GH, MICH, MO, NY, US); *Skutch 3966* (MO, NY, US); *Skutch 4716* (F, US); wet forest at La Hondura, *Standley & Valerio 51900* (US); 13-16 km W of San Isidro along CR 223, 900 m, *Utley 5976* (DUKE); Finca El Quizarrá, 900 m, *Williams et al. 28418* (F, NY). Province unknown: La Funta, *Kupper 148* (M). PANAMA: Chiriquí: moist cliff face along Quebrada Guanabanito, 1 km W of dam at La Represa, *Busey 482* (MO); second growth on Corotu, 6 mi W of airport at Puerto Armuelles, 100-200 m, *Liesner 7* (F, MO, NY, USF); Quebrada Merida, 4 mi S of Puerto Armuelles, 0-100 m, *Liesner 407* (F, MO); between Hato del Jobo and Cerro Vaca, eastern Chiriquí, 700-1000 m, *Pittier 5420* (US); wet mossy bank 6.5 mi S of Volcán, 3300 ft, *Webster 16635* (MO). Coclé: La Mesa above El Valle de Antón, 860-900 m, *Croat 37413* (MO). Veraguas: San Lorenzo, *Seemann 1662* (BM, K).

2. *Begonia sartorii* Liebm., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1852: 14. 1852. TYPE: MEXICO: Veracruz: Chistla pa Mirador, March 1842, *Liebmann s.n.* (Holotype: C!).

   Begonia sarcophylla Liebm. Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1852: 12. 1852. TYPE: MEXICO: Oaxaca: Jocotepec (Chinantla), November 1842, *Liebmann s.n.* (Lectotype: C!).

   Gireoudia lobulata Kl., Monatsber. Königl. Preuss, Akad. Wiss, Berlin 1854: 125. 1854. *nom. nud.*

   Gireoudia sarcophylla (Liebm.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

   Gireoudia sartorii (Liebm.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

   Gireoudia lobulata Kl., Abh. Königl. Akad. Wiss. Berlin 1854: 208. 1855. TYPE: Source unknown: Ex Hort. Bot. Berol., April 1853 (Holotype: B!).

Begonia lobulata (Kl.) A.DC., Prodr. 15(1): 339. 1864.

Begonia cobana C.DC., Bull. Herb. Boiss. II.5: 322. 1908. TYPE: GUATEMALA: Alta Verapaz: Cobán in silva, 1350 m, May 1907, *von Türckheim II 1873* (Lectotype: G!, isolectotypes: US! [2 sheets])

Suffrutescent herbs; *stems* erect, branched or unbranched, 1-2.5 m tall; internodes short to elongate, 1-10 cm X (5) 7-10 (13) mm, moderately to densely lanate when immature, with rufous to ferrugineous trichomes 2-6 mm long intermixed with a sparse covering of minute glandular trichomes, but glabrate with age. *Leaf blades* simple, chartaceous, oblique, asymmetric, reniform, ovate or occasionally oblong, 12-20 (23.9) X 8-16.8 cm, basally broadly but shallowly cordate to narrowly, deeply cordate, apically attenuate-acuminate to abruptly short acuminate or rarely acute, marginally broadly lobed with a principal lobe opposite the petiole insertion, irregularly dentate, ciliate and ciliate-denticulate to ciliate-serrulate, glabrous, glandular or very sparsely pilose basally on principal nerves above and densely lanate below when immature but with age becoming sparsely lanate to pilose, 8-9 (12)-palmatinerved. *Petioles* 5.2-13 (22) cm X 1.5-6 (8) mm, moderately to densely lanate when immature, becoming glabrate to sparsely or moderately pilose but only infrequently densely pilose when mature with rufous to ferrugineous whiplash trichomes 2-4 mm long intermixed with minute glandular trichomes. *Stipules* subpersistent, ascending but spreading to strongly reflexed with age, asymmetric, narrowly ovate to elliptic or lanceolate, 1.9-2.4 (3.2) X 0.6-1 cm, strongly keeled, apically obtuse to acute or acuminate, marginally frequently revolute and entire to ciliate, glabrous to glandular throughout or the keel only pilose to fimbriate-laciniate. *Inflorescences* generally exceeding but occasionally equalling or shorter than the foliage, symmetric to weakly asymmetric, many-flowered, 7.3-16 (23) cm diam. *Peduncles* 7.1-17 (21.5) cm X 2-6 mm, sparsely to moderately glandular-pilose when immature, but glabrate in age. *Bracts* caducous, the lowermost navicular, oblanceolate-obovate, 12-15 X 5.5-8 mm, weakly keeled, apically acute to aristate, marginally entire, glabrous or the keel only very sparingly pilose. *Staminate flowers*: pedicels 7-15 (22) mm long; sepals white to pink, suborbicular to very broadly ovate, 6-10 X 5-10 mm, glabrous to sparingly glandular throughout; petals wanting or 1, rudimentary to oblanceolate, 2-4 X 0.7-2 mm; stamens 11-19; filaments 0.5-1.5 mm long, borne on a low torus; anthers elliptic to oblong-obovate, 1.5-2 (2.2) X 0.6-1 (1.3) mm. *Pistillate flowers*: pedicels 6-10 (18) mm long; sepals colored like staminate sepals, suborbicular, 5-7 X 5-7.5 mm; petals wanting; ovary (4.5) 5.5-8 mm long, glabrous or with a sparse indument of minute glandular trichomes; styles 3, 2-2.5 mm long, connate briefly basally to 3/4 their length; stigmas broadly lunate. *Capsules* with pedicels 12-24 mm long, trilocular, 7-12 mm long; locule chambers externally appearing oblong-elliptic to obovate, (5.5) 6-8 (8.5) X (4.5) 5-6 mm; wings 3, unequal, the largest asymmetrically ovate to broadly elliptic, (7) 9-12 (14) X (7) 8-12 mm, apically obtuse to subacute or truncate, the second broadly lunate to triangular, 4-6 (7) X 7-9 mm, and the third marginiform and shallowly lunate.

DISTRIBUTION AND HABITAT: Southern Mexico to Guatemala in damp and wet forests between 600-2100 m elevation (Fig. 8).

FLOWERING: Flowering occurs from November to early May.

Fig. 8. Distribution of *Begonia crassicaulis* (squares), *B. fonsecae* (triangles) and *B. sartorii* (circles).

DISCUSSION: Liebmann's collections at Copenhagen include two sheets numbered 208 that were annotated as *B. sartorii,* but which are clearly not conspecific. Although both sheets are from the same locality, they were gathered during different months. One specimen dated 3/42 agrees well with Liebmann's original description and our present concept of *B. sartorii.* The second sheet consisting of a single leaf was collected in 11/41. Because of these differences in collection dates, the numbers on the herbarium specimens should not be construed as Liebmann's original collection numbers. Similar disparities have been observed with other Liebmann collections and Oersted collections. Both interestingly have numbers in the same range (i.e. *Oersted* "197" of *B. plebeja*) which appear to have been inscribed on the sheets in the same handwriting. As a result of these factors, I have treated both Liebmann and Oersted collections as lacking collector's numbers. With respect to *B. sartorii,* Liebmann (1852) stated that *B. sartorii* flowered in March, but his description of floral characters was incomplete, indicating that he may have had an immature flowering specimen. The Copenhagen specimen (3/42) is sterile, but earlier type photographs taken by the Field Museum reveal additional material on the sheet with an immature inflorescence. Since Liebmann stated the flowering season as March without indicating any other times, the specimen gathered in 3/42 should be considered the holotype of *B. sartorii.*

Begonia sarcophylla has been treated as synonymous with both *B. sartorii* (A.DC., 1864) and *B. lindleyana* sensu Smith & Schubert (Smith & Schubert, 1946b, 1961) which is herein treated as *B. sericoneura.* Only two specimens potentially from the type collection of *B. sarcophylla* are known, one at Copenhagen and one at Berlin. Although they bear the same label information and number (207), they represent disparate species. The Copenhagen collection of *B. sarcophylla* is clearly identifiable with *B. sartorii,* while the Berlin sheet is a different taxon, *B. pinetorum.* Until recently the only type photographs available of *B. sarcophylla* were of the Berlin specimen which superficially resembles *B. sericoneura.* Since the Copenhagen

specimen best fits the original description, I am selecting it as the lectotype of *B. sarcophylla*.

Included in *B. sartorii* is *B. lobulata* (Kl.) A.DC. Klotzsch (1855) described *Gireoudia lobulata* from a specimen in the Berlin herbarium prepared from cultivated material. When Candolle (1864) included *B. lobulata* in his treatment of the Begoniaceae, he cited *G. lobulata* Kl., the Berlin specimen and *Linden 40*. This latter collection has incorrectly been considered the type of *B. lobulata*. Like *B. lobulata, B. cobana* was previously treated as a synonym of *B. sartorii* by Smith and Schubert (1961) and is well within the variability presently recognized in *B. sartorii*. I have selected as a lectotype for this taxon, *von Türckheim II 1873* from Geneva.

In comparison to many other *Begonia* species, *B. sartorii* is relatively well-collected and existing herbarium material indicates that it is a well-defined species readily distinguished from other Central American taxa by its suffrutescent habit, leaves with a broad but shallow lobe opposite the petiole insertion, lanate to pilose petiolar indument, symmetric cymose inflorescences, stamen number and broadly lunate stigmas. Both primary and secondary floral bracts are conspicuous on immature inflorescences of *B. sartorii*. Based upon inflorescences present on herbarium material, *B. sartorii* appears protandrous with a large portion of the staminate flowers in an inflorescence at anthesis before pistillate flowers mature. Although the vast majority of pistillate flowers and capsules examined lacked bracteoles or bracteole scars on the pedicels, almost half the flowers had rudimentary excrescences on the pedicels in positions that would correspond to bracteolar positions in bracteolate pistillate flowers. Bracteoles when present were small or rudimentary.

Liebmann (1852) associated both *B. sartorii* and *B. multinervia* with *B. dichotoma* Jacq. on the basis of plant habit. Although these taxa are vegetatively similar, they differ in floral characters. The staminate flowers of *B. dichotoma* have 2 sepals and 2 petals while the pistillate flowers have five tepals. In contrast, those of *B. sartorii* and *B. multinervia* regularly have only two sepals. *Begonia sartorii* and *B. multinervia* are, however, similar to each other and have been placed in the same species group with *B. corredorana*. Together with *B. corredorana*, they share a common habit, narrowly ovate-lanceolate stipules, symmetric inflorescences, generally apetalous flowers and similar capsules. The differences between these three taxa are summarized in Table 3. In both *B. sartorii* and *B. multinervia*, the leaves are typically glabrous adaxially and the bracts are valvate. *Begonia sartorii* differs from *B. multinervia* in its ciliate and ciliate-denticulate leaf margins, lanate petiolar indument of whiplash trichomes, fewer stamens and lunate stigmas. In addition to vestiture, stamen number, and stigma form, *B. sartorii* can be distinguished from *B. corredorana* by its glabrous adaxial leaf surfaces, subpersistent stipules and larger sepals.

SPECIMENS EXAMINED: MEXICO. Chiapas: paraje of Yehts 'UK'um, Municipio of Tenejapa, 4500 ft, *Breedlove 7484* (DS, F, US); road from Bochil to Simojovel, 4 mi NE of Bochil, Municipio of Bochil, 4500 ft, *Breedlove 8834* (DS, US, WIS); E base of Cerro Tres Picos near Cerro Bola logging road SW of Colonia Agrónomos Mexicanos, Municipio de Villa Corzo, 1500 m, *Breedlove & Thorne 30213* (DS, MO); 16 km NW of Rizo de Oro, logging road to Colonia Figaroa, Municipio of Cintalapa, 1600 m, *Breedlove 31336* (DS, MEXU, MICH, MO); 7 km NE of Bochil, road to Simojovel, Municipio of Bochil, 1250 m, *Breedlove & Smith 32305* (DS, MEXU); Cerro Brujo between Ranchos Concepción and Olinipo, *Langman 3875* (US); forêts du pins, without further locality, *Linden 40* (K, P); Río Hondo 4 mi N of Jitotol on road

to Pueblo Nuevo Solistahuacán, Municipio of Jitotol, 5500 ft, *Raven & Breedlove 19963* (DS, F, US); Ocosingo, *Seler & Seler 2618* (B, GH); paraje of Mahosik', Municipio of Tenejapa, 4800 ft, *Shilom Ton 1923* (DS, MEXU, NY, US); paraje of Yash'anal, Municipio of Tenejapa, 2000 m, *Shilom Ton 2084* (DS, MICH, MSU); *Shilon Ton 2089* (NY, US); near Rancho Mumuntik near Ocosingo, Municipio of Ocosingo, 4200 ft, *Shilom Ton 3519* (DS, MEXU, MSC, NY, US); near Rancho Viejo of Finca Prusia, Municipio Angel Albino Corzo, 2400 ft, *Shilom Ton 3529* (DS, DUKE, F, MICH). Guerrero: about 14 km al SSW del Campamento El Gallo, el camino a Atoyac, 1950 m, *Rzedowski & McVaugh 63* (MICH). Oaxaca: Hwy 175, 55 mi S of Miahuatlán, 1540 m, *Croat 46104* (MO); Finca Soledad, *Alexander 564* (NY); La Soledad, *Ernst 2598* (MEXU, US); Chinantla, *Liebmann s.n.* (C). Veracruz: Valle de Córdova, Trinidad, *Bourgeau 2100* (B, GH, M, MEXU, P, US); *Purpus 6351* (BM, MO, UC, US); Zacuapan, *Purpus 7758* (GH, MO, UC, US); without locality, *Liebmann s.n.* (B). GUATEMALA. Alta Verapaz: Damp woods, Cobán, 4300 ft, *Hunnewell 17175* (GH); 3 km de Villa Hermosa, 1400 m, *Molina & Molina 12374* (F, NY); Cobán, 1260-1440 m, *Standley 69451* (F); *von Türckheim 1159* (B, GH, P, US); *von Türckheim II 1619* (BR, G, US); hills about 5 km N of San Pedro Carchá, 1200 m, *Williams et al. 40220* (F, MO); Sierra Chamá, Río Cobán, about 5 km from Cobán, 1300 m, *Williams et al. 40633* (F, NY, US). Baja Verapaz: without further locality, *Seler & Seler 3376* (B, GH); N of divide N of Santa Rosa, 1650 m, *Standley 69913* (F); Sierra de las Minas, near Pantín, 1600-1800 m, *Williams, Molina & Williams 42130* (DUKE, F). Chiquimula: Montaña Nonojá, 3-5 mi E of Camotán, 600-1800 m, *Steyermark 31684* (F). Huehuetenango: opposite river from Finca Soledad, 5 mi SE of Barillas, Sierra de los Cuchumatanes, 1150 m, *Steyermark 49502* (F, GH). Zacapá: Rillito del Volcán de Monos, Volcán de Monos, 1150-2100 m, *Steyermark 42385* (F, GH).

3. *Begonia corredorana* C.DC., Candollea 2: 227. 1925. TYPE: COSTA RICA: Llanos de Corredor, March 1897, *Pittier 10954* (Holotype: BR!; isotypes: CR!, K!, US!).

   Begonia valerii Standl., Jour. Wash. Acad. Sci. 17: 313. 1927. TYPE: COSTA RICA: Guanacaste: El Arenal, 485-600 m, January 18-19, 1926, *Standley & Valerio 45245* (Holotype: US!).

Suffrutescent herbs; *stems* ascendant, generally unbranched, 0.5-2.5 m tall; internodes short to elongate, 0.9-11.5 cm X 3-9 mm, moderately to densely villous with deep pink-red to cinnamon or rufous spreading to retrorse trichomes 0.6-3 mm long, frequently with minute glandular trichomes interspersed. *Leaf blades* simple, membranaceous to chartaceous, transverse or oblique, asymmetric, ovate or obovate to oblong-elliptic or suborbicular, (13.5) 16-28.2 X (7.4) 9-15.5 (19) cm, basally broadly but shallowly cordate, only infrequently narrowly, deeply cordate, apically attenuate-acuminate, marginally occasionally with a broad but shallow lobe opposite the petiole insertion, obsoletely to markedly undulate, ciliate-denticulate and ciliate, sparsely to moderately glandular-hirsute above and beneath but with trichomes most dense on principal nerves below, palmately 10-13-nerved. *Petioles* light green, occasionally suffused with red, 7-10 cm X 2-3 mm, moderately to densely villous with spreading rounded or flattened trichomes 1-3 mm long, only infrequently glabrate with age. *Stipules* caducous, asymmetric, lanceolate, 1.8-2.5 X 0.6-0.8 cm, strongly keeled, apically obtuse to acute, marginally entire, sparsely to densely villous throughout. *Inflorescences* typically exceeding the leaves, many-flowered, laxly to densely cymose, symmetric to only slightly asymmetric, (6.5) 13-25 cm diam. *Peduncles* (12.3) 18.5-35.5 cm X 2.5-5 mm, only sparsely glandular-pilose, becoming glabrate with age. *Bracts* fugacious, the lowermost unknown, upper bracts navicular, broadly ovate to suborbicular or obovate, apically rounded to subacute, marginally entire, glabrous to sparsely pilose or glandular throughout. *Staminate flowers*: pedicels (3.5) 5-10 (16) mm long; sepals white to pale pink, ovate or broadly ovate to subordicular, 2.5-6 (7) X 2.5-6 mm, glabrous or pilose, with glandular

trichomes intermixed; petals wanting; stamens 16-41; filaments 0.5-1.6 (2) mm long, inserted on a low to raised torus; anthers oblong-obovate, (0.3) 0.5-1 (1.3) X (0.3) 0.5-0.7 (0.9) mm. *Pistillate flowers*: pedicels 5-12 (20) mm long; sepals colored like staminate sepals, suborbicular to obovate, 3-7 X 3-7.5 mm, glabrous to glandular-pilose; petals wanting; ovary 3-4 mm long, glabrous to glandular throughout and, except for the wings, often pilose, especially basally; styles 3, 1.5-2 mm long, connate only briefly basally; stigmas bicornute. *Capsules* with pedicels (7) 9-19 (23) mm long, trilocular, 5-9 mm long; locule chambers externally appearing broadly elliptic to suborbicular or transversely broadly elliptic, 4.5-7 (8) X 3-6 (7) mm; wings 3, unequal, the largest asymmetrically narrowly ovate to oblong or subdolabriform, (12) 14-19 (22) X (7) 9-11 mm, apically subacute to obtuse or truncate, the second and third frequently asymmetric, shallowly lunate or lunate-triangular.

DISTRIBUTION AND HABITAT: Costa Rica and Panama from 20-900 m. *Begonia corredorana* forms small populations on steep, wet slopes and occasionally on wet road banks along Costa Rica's Caribbean and Pacific slopes. In Panama it is most frequently collected on the Burica Peninsula near the Costa Rican border but recently has been found in the Darien (Fig. 9).

FLOWERING: December to April.

DISCUSSION: The characteristics which distinguish *B. corredorana* include its caulescent, non-rhizomatous habit, villous internodes and petioles, caducous stipules, generally unlobed leaves with ciliate-denticulate margins and hirsute adaxial surfaces, lax, many-flowered symmetric inflorescences, bicornute stigmas and unequal capsule wings.

Subtle differences exist among populations of *B. corredorana* from different parts of Costa Rica. Those from the Valle del General are similar to material from Panama in possessing smaller, glabrous sepals, fewer stamens, and shorter pistillate pedicels than *Utley 6071* from near Turrialba, *Standley & Valerio 46963* from Pejivalle or *Lent 2354* from Taus along Costa Rica's Caribbean slopes or *Utley 5972* from a Pacific cloud forest in the mountains between Dominical and San Isidro. Sepals on these specimens

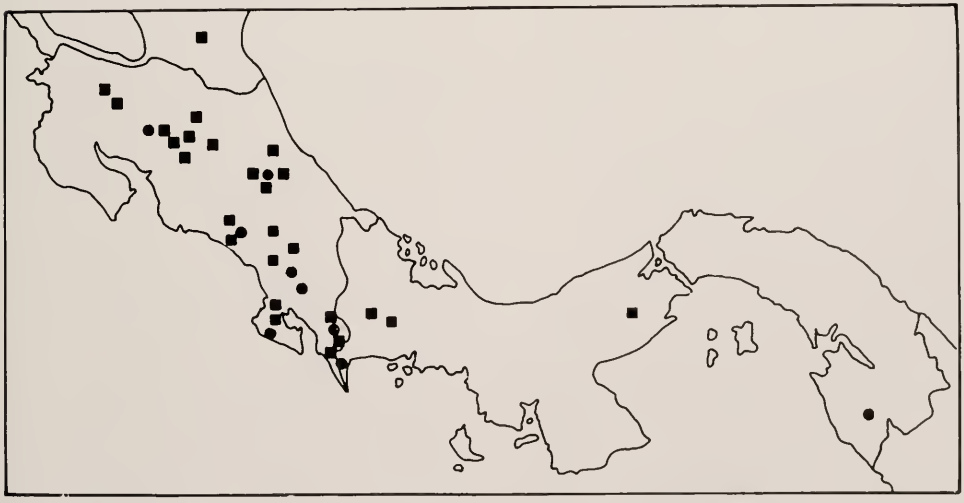

Fig. 9. Distribution of *Begonia corredorana* (circles) and *B. multinervia* (squares).

were sparsely pilose and the inflorescences were characterized by highly reduced or aborted ultimate internodes, much like the ultimate internodes associated with *B. involucrata,* but no other species in sect. *Gireoudia.* Correlated with the aborted ultimate internodes appears to be the elongate pistillate pedicels, as they are observed only in populations of *B. corredorana* and in *B. involucrata.* Since bracts of *B. involucrata* and a closely related species, *B. broussonetiifolia,* are unique in sect. *Gireoudia,* it is unfortunate that bracts of *B. corredorana* are unknown and unavailable for comparison with these taxa. *Begonia corredorana* differs from *B. involucrata* and *B. broussonetiifolia* in its unlobed leaf blades. Material from El Arenal which includes the type of *B. valerii* is similar in size and stamen number to populations of *B. corredorana* previously cited, but has glabrous sepals and unaborted ultimate inflorescence internodes like populations from the Valle del General. Inflorescences of these specimens differ from both other forms in their somewhat persistent secondary floral bracts which in all other material appear to be caducous or fugacious. The significance of these differences is presently not well understood and may in part be a reflection of the tendency of *B. corredorana* to form small, geographically isolated populations. Further evaluation of these characters must await extensive collections from El Arenal and the Caribbean slopes.

Begonia corredorana is part of a species group which includes *B. sartorii* and *B. multinervia.* These species are suffrutescent herbs and, with the exception of *B. sartorii* from Guatemala and Mexico, have induments comprised of villi and bicornute stigmas. *Begonia corredorana* shares with *B. multinervia* similar stipules and leaf form, stamen number, bicornute stigmas, petiolar indument, and a similar distribution. Many populations of *B. corredorana* also have symmetric, cymose inflorescences with elongate internodes like *B. multinervia.* The major distinctions between these taxa are *B. corredorana*'s hirsute upper leaf surface, typically green leaves, and ciliate-denticulate and cilate leaf margins. In *B. multinervia* the adaxial surface is glabrous while the margination is entire to undulate or irregularly denticulate but not ciliate and the leaves are frequently deep maroon beneath (Table 3). *Begonia corredorana* differs from the remaining member of the multinervia species group, *B. sartorii,* primarily in its villous indument, hirsute adaxial leaf surfaces, more numerous stamens and bicornute stigmas. Like *B. multinervia, B. sartorii* has glabrous upper leaf surfaces, but stands apart from both *B. multinervia* and *B. corredorana* in its leaf blades with generally a broad lobe opposite the petiole insertion, whiplash trichomes, fewer stamens and lunate stigmas (Table 3).

Begonia corredorana has been observed growing in mixed populations with *B. multinervia* in the Fila Cal between Agua Buena and Villa Neilly, but no evidence is available to suggest that they hybridize in regions of sympatry. In the Valle del General near the Río Claro, individuals of *B. corredorana (Burger & Matta 1800)* have been collected apparently growing sympatrically with *B. sericoneura (Burger & Matta 1816). Burger & Matta 1820* which was also gathered at the same locality is morphologically intermediate between *B. corredorana* and *B. sericoneura.* It resembles *B. corredorana* in its coarsely villous stems and petioles, but differs in its marginally doubly dentate to doubly serrate leaf blades and inflorescences with large, bracteolate pistillate flowers

with broad, lunate stigmas. In these features the intermediate more closely resembles *B. sericoneura*. Although capsules were lacking from *Burger & Matta 4820*, wing characters can be inferred from mature pistillate flowers. The primary wings are broadly triangular and are similar to the typical *B. sericoneura* wing form; the secondary wings are also well-developed, which is unusual in *B. corredorana*, but common in *B. sericoneura*.

SPECIMENS EXAMINED: COSTA RICA. Cartago: Río Pejibaye, 0.7 km S of Taus, 740 m, *Lent 2354* (F, MO, NY); Pejivalle, 900 m, *Standley & Valerio 46963* (US); *Standley & Valerio 47112* (US); about 16 km NE of Turrialba, rd to Siquirres, 900 m, *Utley 6071* (DUKE, F, US). Guanacaste: El Arenal, 485-600 m, *Standley & Valerio 45287* (US). Limón between Limón and Siquirres nearer to Siquirres, Río Madre de Dios, *Burger, Visconti & Gentry 10516* (F). Puntarenas: forested hills above Palmar Norte de Osa, 500 m, *Allen 5860* (F); original forest about 1 km SE of Río Claro, 20-30 m, *Burger & Matta 4800* (CR, F, NY); *Croat 32943* (MO, US); Osa Peninsula, Corcovado National Park, primary forest 0-1 km upstream from Los Chiles, 300-400 m, *Liesner 3124* (MO). San José: near Alto San Juan on rd to Dominical, 900 m, *Molina et al. 18110* (F, US); basin of El General, 675-900 m, *Skutch 4733* (CR, F, GH, MO, NY, US); wet roadbanks along rd to Dominical, 900 m, *Utley 5972* (CR, DUKE, F, GH, MO). PANAMA. Chiriquí: Burica Peninsula, San Bartolo, 12 km W of Puerto Armuelles, 200 m, *Busey 712* (F, GH, MO, NY); Rabo de Puerco, 8 km W of Puerto Armuelles, 50-150 m, *Croat 21974* (F, MO, NY, USF); primary forest, San Bartolo Limite near Costa Rican border, 400-500 m, *Croat 22189* (MO); 7 mi W of Puerto Armuelles, 120 m, *Croat 35046* (MO). Darién: Río Tacarcuna, vicinity of old Tacarcuna village, 580 m, *Gentry & Mori 13565* (MO, US).

4. *Begonia broussonetiifolia* A.DC., Ann. Sci. Nat. IV. 11: 133. 1859. TYPE: GUATEMALA: without further locality, 1841, *Friedrichsthal 1034* (Lectotype: W!, isolectotypes: F-fragments!, W! [2 sheets]).

Suffrutescent herbs; *stems* frequently deep red, slender, 0.5-1.0 m tall; internodes generally elongate, (0.9) 1.8-4.4 (8.5) cm long X (2) 3-6 mm, densely tomentose, but only sparingly so with age, with trichomes 1.5-2.5 mm long, often intermixed with minute glandular trichomes. *Leaf blades* simple, oblique to transverse, asymmetric, elliptic, ovate or obovate, (11.5) 12.5-18 X 6.4-10 (11.5) cm, basally broadly to narrowly shallowly cordate, apically attenuate-acuminate, marginally deeply sinuate-lobed subapically with a large, well-developed attenuate-acuminate lobe oblique to the leaf base, occasionally a second lobe present between the leaf apex and base, obsoletely undulate, frequently broadly crenulate, infrequently ciliate, denticulate or serrulate throughout, but apices of major lobes often ciliate-denticulate to ciliate-serrulate, glabrous to sparingly hirtellous throughout or principal nerves only hirtellous above, and beneath sparsely to moderately hirtellous in intercostal regions but densely tomentose on principal nerves, palmately 9-11-nerved. *Petioles* often deep red, slender, 6.8-11 (16) cm X 1-2.5 (3) mm, densely tomentose, with villi (0.5) 1-1.5 (2) mm long, often with minute glandular trichomes intermixed, becoming sparingly tomentose with age. *Stipules* persistent, ascending but spreading to reflexed with age, narrowly ovate to lance-triangular, 1.1-2 X 0.7-1.1 (1.4) cm, weakly keeled, apically obtuse to acute, marginally entire, glabrous to sparingly puberulous throughout or only along the keel. *Inflorescences* generally exceeding the leaves, symmetric to weakly asymmetric, laxly cymose, many-flowered, 4.5-9 (13) cm diam. *Peduncles* green suffused with pink, (14.6) 17.5-27.5 (29) cm X 2.5-3.5 mm, sparingly to densely tomentose, with minute glandular trichomes often intermixed. *Bracts* caducous, light green, the lowermost pair with the outer completely encircling the inner, glabrous to sparingly pilose throughout. *Staminate flowers*: pedicels 7-11 mm

long; sepals white to pale pink, suborbicular to broadly oblong or ovate, 6-8 (11) X 6-9 mm, externally glabrous, glandular, sparsely pilose or glandular-pilose throughout; petals wanting; stamens 21-34; filaments 0.4-1.5 mm long, borne on a low torus; anthers oblong-elliptic to obovate, 1-1.6 X 0.5-0.8 mm. *Pistillate flowers*: pedicels 6-9 (14) mm long; bracteoles wanting or rudimentary and fugacious; sepals colored like staminate sepals and with a similar indument, transversely elliptic to broadly obovate, 3.5-9 (10) X 7-9 (11) mm; petals generally wanting, but when present, 1, oblanceolate, 4.5 X 2 mm; ovary 3.5-5.5 mm long, glabrous to sparingly glandular throughout but frequently sparsely pilose basally; styles 3, 1.5 mm long, connate 1/3-1/2 their length; stigmas bicornute. *Capsules* with pedicels 11-18 (21) mm long, trilocular, (5) 6-8 mm long; locule chambers externally appearing cordate to oblong, 4.5-6.5 X 4-6.5 mm; wings 3, unequal, the largest often asymmetric, oblong-elliptic or narrowly ovate-triangular, (11) 12-15 X (7) 8-10 (11) mm, apically oblique, truncate, obtuse or subacute, the second broadly lunate to asymmetrically triangular, 4-7 X 6-7 mm, the third marginiform or subequal to the second.

DISTRIBUTION AND HABITAT: *Begonia broussonetiifolia* has been reported from Guatemala, Nicaragua and Costa Rica. In Costa Rica this species is restricted to the Cordillera de Tilarán where it occurs in cloud forests between 700-1600 m elevation. While *B. broussonetiifolia* is often gregarious, forming large colonies on steep, wet forested slopes, it is not an aggressive colonizer and is absent from weedy habitats (Fig. 10).

FLOWERING: Populations of *B. broussonetiifolia* appear to flower sporadically throughout the year, but flower most profusely from December to February.

DISCUSSION: The type of collection from Guatemala and Wright's collection from Nicaragua are the only collections of *B. broussonetiifolia* from these countries and were made over 100 years ago. More recent field work in these countries has failed to substantiate the Guatemalan and Nicaraguan distributions of this taxon and it is with reservation that they are included here. I have selected one of the three Friedrichsthal specimens at W as the lectotype of *B. broussonetiifolia*.

Begonia broussonetiifolia is morphologically most similar to *B. involucrata* and most recently has been treated as a synonym of this taxon by Smith and Schubert (1958, 1961). It shares with *B. involucrata* its suffrutescent habit, sinuate-lobed leaves, unique inflorescence bracts in which the outer encircles the inner, comparable stamen number, bicornute stigmas and similar capsules. *Begonia broussonetiifolia* also has a tomentose petiolar indument superficially similar to that observed on individuals from many populations of *B. involucrata*. It is, however, comprised of fine sericeous villi and not whiplash trichomes. The major differences in these taxa include the more slender stems of *B. broussonetiifolia*, its persistent, spreading to reflexed stipules that are generally smaller than those observed on *B. involucrata*, elongate inflorescence internodes and shorter pistillate pedicels (Table 4). The leaves of *B. broussonetiifolia* are also subtly different and are more deeply sinuate-lobed with generally only one large secondary lobe, so that the leaves appear bilobed. The margins are only rarely ciliate and ciliate-denticulate, but just behind the apices of the blade and lobes, they may be both weakly ciliate and ciliate-denticulate. Leaves of *B. involucrata*

TABLE 4. Morphological comparison of *Begonia broussonetiifolia* and *B. involucrata*.

	B. broussonetiifolia	*B. involucrata*
Upper leaf surface	glabrous to hirtellous	hirtellous or scabrous
Leaf size (cm)	(11.5)12.5-18 X 6.4-10(11.5)	(8.7)11.2-27.5(33) X (5.6)8.8-17.2(22.3)
Leaf margination	deeply sinuate-lobed	sinuate-lobed, doubly dentate, ciliate and ciliate-denticulate
Petiole length (cm)	6.8-11(16)	(1.7)8-20(37.2)
Petiolar indument	tomentose	villous to tomentose
Trichome type	sericeous villi	coarse to sericeous whiplash trichomes
Inflorescence internodes	elongate	reduced to aborted
Stamens	21-34	(16)20-41(62)
Pistillate pedicels (mm)	6-9(14)	(6)16-25(30)
Stigmas	bicornute	bicornute

frequently have several secondary lobes and are coarsely denticulate-serrulate or ciliate-denticulate and often doubly dentate to serrate. *Begonia broussonetiifolia* is most abundant in wet cloud forests at elevations under 1600 m (700-1600 m) while *B. involucrata* is rarely found in cloud forests, preferring instead wet montane forests between 1400-2000 m elevation, although it grows at lower and higher elevations.

SPECIMENS EXAMINED: NICARAGUA: Without further locality, *Wright s.n.* (GH, NY, US). COSTA RICA: Alajuela: Los Angeles y La Paz de San Ramón, *Brenes 6104* (CR, F, GH, NY); Piedades Norte y Los Angeles de San Ramón, *Brenes 6719* (CR, F, NY); Cataratas de San Ramón, *Brenes 13475* (F, NY); upper drainage of Río Peñas Blancas below Monteverde Cloud Forest Reserve, 1250-1350 m, *Burger, Visconti & Burger 10736* (F); between San Ramón and La Balsa at Angeles Norte, 1250 m, *Croat 46853* (MO); N of San Ramón on gravel road to Angeles Norte and La Balsa, 1200 m, *Croat 46864* (MO); San Antonio de Zarcero, 1550 m, *Smith 282* (MICH, US); Atlantic cloud forest, Zarcero, *Smith H250* (F); Pacific cloud forest zone, San Luis de Zarcero, 1600 m, *Smith H568* (F, MO); *Smith NY1177* (GH, NY); about 2 km N of La Balsa de San Ramón, *Utley 5816* (DUKE). Puntarenas: about 2 km SE of Monteverde, 1500-1550 m, *Burger & Gentry 8556* (CR, F).

5. *Begonia involucrata* Liebm., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1852. 15. 1852. TYPE: COSTA RICA: In monte Candelaria, 6000 ft, February 1847. *Oersted s.n.* (Lectotype: C!; isolectotypes: B!, C!).

   Gireoudia involucrata (Liebm.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

   Gireoudia laciniata Kl., Abh. Königl. Akad. Wiss. Berlin. 1854: 205. 1855. TYPE: CENTRAL AMERICA: without further locality, described from cultivated material grown by Mathieu at Berlin from seed sent by Warscewicz (Holotype: B!).

   Begonia laciniosa A.DC., Prodr. 15(1): 340. 1864.

Suffrutescent herbs; *stems* erect, unbranched, 1-2 m tall; internodes generally elongate, but occasionally short, (0.6) 1.3-6.3 (9) X 0.6-1.2 cm, lenticellate, densely tomentose to densely coarsely villous, becoming moderately to densely

sericeous or moderately villous with age, with trichomes 1-2 mm long, often intermixed with minute glandular trichomes. *Leaf blades* simple, coriaceous to subcoriaceous, oblique to transverse, asymmetric, oblong, broadly elliptic, ovate or obovate, (8.7) 11.2-27.5 (33) X (5.6) 8.8-17.2 (22.3) cm, basally deeply narrowly cordate or infrequently broadly but shallowly cordate, lobes often overlapping, apically attenuate-acuminate, marginally strongly sinuate-lobed with 2 or more well-developed often cuspidate lobes, generally 1 on either side of the apex, the third, when present, on the side of the leaf opposite the petiole about 2/3 the distance back from the apex, doubly dentate to doubly serrate, coarsely ciliate-denticulate to ciliate-serrulate and ciliate, moderately to densely hirtellous above and beneath, 9-14-palmatinerved. *Petioles* light green, (4.7) 8-20 (32.7) cm X 2-4 (6) mm, densely pilose to tomentose, with soft to coarse whiplash trichomes 1-3 mm long, frequently intermixed with minute glandular trichomes. *Stipules* caducous or infrequently deciduous, subelliptic to lance-triangular, (1.2) 2-3.2 (3.8) X 0.8-1.3 (1.6) cm, strongly keeled, apically obtuse to subacute, marginally entire, sparingly to moderately pilose throughout or the lamina glabrous and keel sparingly pilose. *Inflorescences* greatly exceeding the foliage, symmetric to weakly or moderately asymmetric, characteristically densely cymose, many-flowered, with generally the upper branches, but frequently both upper and lower branches greatly reduced in length, making the inflorescence strongly congested distally, (3.5) 5.5-18 (29) cm diam. *Peduncles* light green, (14) 23-47.5 cm X (2) 3-6 (9) mm. *Bracts* caducous, light green, the lowermost with the outer completely encircling the inner in bud, subequal, broadly navicular, broadly ovate to transversely elliptic, (1.2) 1.5-3 (3.8) X 1.6-2.5 (3.9) cm, apically attenuate-acuminate, marginally entire, glabrous to sparingly pilose. *Staminate flowers*: pedicels (0.9) 1.2-2.3 cm long; sepals white or rarely suffused with pink, ovate to broadly oblong-elliptic, 8-14 X 6.5-10 mm, glabrous but infrequently glandular or sparingly pilose; petals wanting, rudimentary or 1-2, white, oblanceolate to narrowly obovate, 3-7 X (0.8) 1-2 mm; stamens (16) 20-41 (62); filaments (0.7) 1-2 mm long, borne on a very low torus; anthers 0.9-1.3 X 0.5-0.8 mm. *Pistillate flowers*: pedicels (0.6) 1.6-2.5 (3) cm long; bracteoles wanting; sepals colored like staminate sepals, broadly elliptic to transversely elliptic or suborbicular, (4.5) 6-9 (11) X (3) 4-9 (10) mm; petals generally wanting, but when present, 1, white, oblanceolate, 3-4.5 X 0.6-1.2 mm; ovary 4-7.5 mm long, glabrous or sparsely puberulous basally; styles 3, 1.5-2.6 mm long, fused to 1/2 their length; stigmas bicornute. *Capsules* with pedicels (1.5) 2.1-3.6 (6) cm long, trilocular, (6) 7-11 mm long; locule chambers externally appearing oblong-elliptic, suborbicular, transversely elliptic or obovate, 5-9 X 4-7 mm; wings 3, unequal, the largest asymmetric, oblong, ovate, suborbicular or narrowly dolabriform, (8) 11-23 X (7) 8.5-13 (16) mm, the second marginiform to broadly but shallowly lunate, (4) 5.5-13 X 5-9 mm, the third marginiform.

DISTRIBUTION AND HABITAT: Known only from Costa Rica and the Chiriquí region in western Panama. The Guatemalan and Nicaraguan distributions included by Smith and Schubert (1958, 1961) are based upon specimens now referred to *B. broussonetiifolia*. While *B. involucrata* has been collected at elevations between 1050-3200 m, this species is most common at elevations from 1400-2000 m and occurs most frequently in the cool, seasonally drier, wet

lower montane and montane Pacific slopes of the cordilleras. It often forms local, large colonies on steep forested slopes and along forested stream banks (Fig. 10).

FLOWERING: Most profuse from December to April and only sporadically during other months.

DISCUSSION: I have selected one of the two Oersted collections from Copenhagen gathered in February 1847 as the lectotype of *B. involucrata*. The most striking features of *B. involucrata* which readily separate it from other Mesoamerican begonias are its densely cymose inflorescences with the upper and frequently lower internodes greatly reduced in length, and long pistillate and capsular pedicels. The extent of internode reduction is variable not only within populations of *B. involucrata*, but also within individual plants. A feature which *B. involucrata* shares with *B. broussonetiifolia* but is unknown from other species in the section is an unusual inflorescence bract form in which the outer of the lowermost pair of fleshy bracts completely encloses the inner bract.

Leaves of *B. involucrata* have been characterized as sinuate-lobed but the number of lobes per leaf and their depth is variable within individual plants (*i.e. Burger & Liesner 7043*). Similar variation has been observed in other species with lobed leaves in sect. *Gireoudia*. Two different petiole and internode indu-ments have been observed in *B. involucrata*. In specimens gathered in the Cordillera de Talamanca south of Villa Mills and north of San Isidro along the Interamerican Highway in Costa Rica, the internodes and petioles are covered with coarse whiplash trichomes while in all other areas in Costa Rica and Panama, the indument is tomentose, consisting of fine whiplash trichomes. In leaf form, inflorescence form, stigma shape, stamen number and the sizes of various morphological parts, the populations were indistinguishable.

Begonia involucrata is most closely allied with *B. broussonetiifolia* and this relationship is pursued further in the discussion of *B. broussonetiifolia*. The unusual internode reduction or abortion characteristic of *B. involucrata* has been observed in only one other species in the

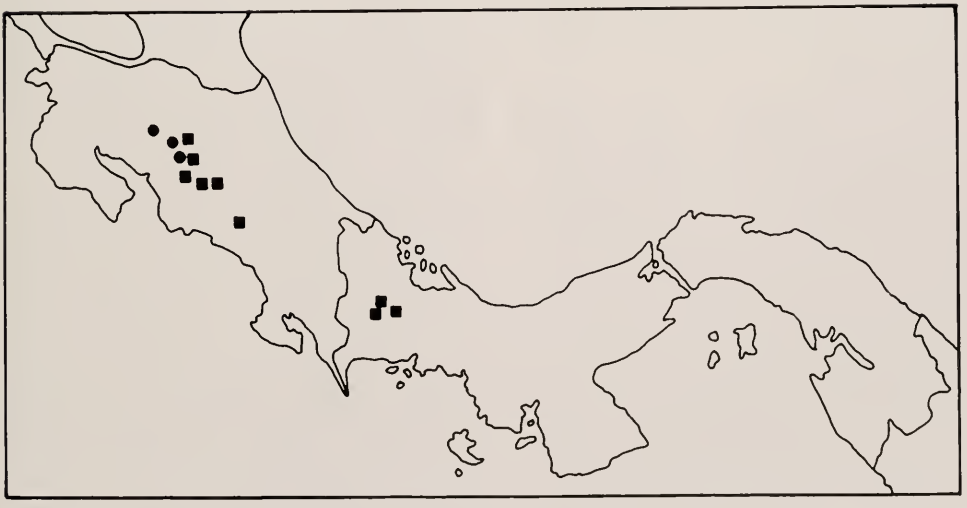

Fig. 10. Distribution of *Begonia broussonetiifolia* (circles) and *B. involucrata* (squares).

section, *B. corredorana*. Although some populations of *B. corredorana* share this unusual inflorescence internode reduction with *B. involucrata*, these taxa can be readily distinguished from each other by a number of characteristics, including elevational distribution. The leaves of these two taxa differ significantly in margination, with those of *B. involucrata* having strong sinuate-lobed margins while those of *B. corredorana* are only ciliate-denticulate with an occasional broad, but shallow rounded lobe opposite the petiole insertion. Pistillate pedicel length also differs markedly between these taxa, with those of *B. involucrata* generally being much longer than those of *B. corredorana*. The relationships between *B. involucrata* and *B. broussonetiifolia* and *B. multinervia* are discussed under these taxa.

Begonia involucrata occurs in mixed populations with *B. strigillosa* on the slopes of Volcán Barba, but there is little opportunity for hybridization since *B. strigillosa* flowers during the rainy months from September to November in this region. Even if flowering were concurrent, the potential for hybridization should be greatly reduced because of differences in stature between these species resulting in positive assortative pollination.

SPECIMENS EXAMINED: COSTA RICA: Alajuela: La Palma de San Ramón, 1190 m, *Brenes 3805* (F); *Brenes 5407* (CR, F, NY); Cataratas de San Ramón, *Brenes 13485a* (NY); La Palma de San Ramón, *Lent 2369* (CR); Zarcero, 5300 ft, *Smith A377* (F); *Smith H10* (F, MO); *Smith 144* (US); *Smith 145* (US); *Smith 146* (US); *Smith 287* (F); Caribbean cloud forest, Zapote de San Carlos, 2000 m, *Smith PC288* (F); *Smith H547* (F, GH); cloud forest, Caribbean watershed, Tapesco de Zarcero, 1600 m, *Smith NY1231* (F, NY); cloud forest, San Luis de Zarcero, 1525 m, *Smith P2056* (GH, US); Pacific cloud forest, 6 mi SW of Zarcero, *Smith RZ13* (US); La Ventolera on S slope of Volcán Poás, 1700 m, *Standley 34563* (US); near Tapesco River, Cordillera Central, about 10 km N of Zarcero, 1600 m, *Williams et al. 28921* (F, GH, NY, US). Cartago: Cartago, 4250 ft, *Cooper 5777* (F, US); N slope of Cerro Carpintera above battlefield at Laguna de Ochomogo, 1560-1700 m, *Dodge & Thomas 6153* (GH, MO); woods 4 km SW of Tobosi, 1700 m, *Lent 3169* (US); La Carpintera, *Standley 34241* (US); *Standley 35489* (US); N of Cartago along Río Reventado, 1460 m, *Standley & Valerio 49379* (US); *Standley 49548* (US); forest edge, Carpintera, *Stork 1080* (F); *Williams 16161* (US); *Williams 19137* (US). Heredia: Río Porrosatí, 1800 m, *Leon 522* (CR, F); 1.7 km W of Porrosatí along CR114 to Sacramento, 1900-2000 m, *Utley & Utley 4567* (CAS, CR, DUKE, F, MEXU, MICH, MO, NY, US). Puntarenas: Pacific watershed, about 2 km SE of Monteverde, 1500-1550 m, *Burger & Gentry 8678* (F, MO). San José: Tarbarcia, 1600 m, *Alfaro 13* (F); San Isidro de Coronado, *Alfaro 32393* (US); *Allen 537* (F); *Allen 539* (F, MO); 2-6 km S of Higuito on drier slopes of Altos de Tablazo, 4500-5800 ft, *Almeda, Nakai & Utley 3733* (CAS); near San Antonio de Escazú, *Barkley 41549* (US); 25 km N of San Isidro de El General, 1800 m, *Burger & Liesner 7043* (CR, F, MO, NY); *Burger & Baker 10077* (NY); Aserrí, *Hunnewell 16666* (GH); *Hunnewell 16667* (GH); Quebrada de los Yases, entre La Guaria y Palmilera, Dota, 1700 m, *Jiménez 1454* (CR, F, LL, NY); Alajuelita, ca 4 km of San José, 1550 m, *Kuhlbier 104* (CR); Escazú, *Nickle & Barkley s.n.* (MO); monte Candelaria, 6000 ft, *Oersted s.n.* (C); Curridabat, 1200 m, *Pittier 67* (BR, F, US); Cantina La Lucha, above Las Nubes, *Schubert & Rogerson 633* (US); above Aserrí *Schubert & Rogerson 699* (US); ravine above Las Nubes, *Schubert 1022* (F); riverside thicket, vicinity of El General, 1560 m, *Skutch 2988* (GH, MO, NY, US); Piedra Blanca, 1900 m, *Solis 165* (CR, F, MO); Cerros de Escazú, *Solis 271* (F); *Standley 32436* (US); *Standley 32503* (US); between Aserrí and Tarbaca, 1600-1900 m, *Standley 34107* (US); *Standley 41407* (US); Santa María de Dota, 1500-1800 m, *Standley 41838* (US); moist thicket along Río Blanco NE of El Copey, 1800-1900 m, *Standley 41888* (US); Santa María de Dota, 1500-1800 m, *Standley 42388* (US); *Standley & Valerio 44065* (US); wet forest, Zurquí, 2000 m, *Standley & Valerio 48137* (US); ruisseau dans les llanos d'Alajuelita, *Tonduz 1506* (BR, CR, US); Santa María de Dota, 1300 m, *Tonduz 2361* (BR, CR); forêts du Copey, 1800 m, *Tonduz 11809* (CR, US); Santa Rosa de Copey, *Tonduz 12178* (CR, US); slopes 5 km SE of Hiquito, on Calle Tablazo, Altos de Tablazo, 1800-1900 m, *Utley & Utley 3857* (CR, DUKE, F, MEXU, MO, NY, US); between Cascajal and San Isidro de Coronado, 500-6000 ft, *Utley 5714* (DUKE, MO, US); streambanks SW of Cerro Daser, Cerros de Escazú, 2000 m, *Utley 5744* (BR, CAS, CR, DUKE, F, GH, MO, TEX); 4 km SE of Hiquito, Altos de Tablazo,

Utley 5771 (B, C, CR, DUKE, F, G, K, MICH, MO, NY, US, W); *Utley 5776* (DUKE, F, GH, MO, US); 26 km S of La Georgina along Interamerican Hwy, 1600-1800 m, *Utley 6103* (DUKE); 16 mi N of San Isidro del General near Río Paynar, 1580 m, *Wilbur & Luteyn 18997* (DUKE); near Tarbaca, about 15 km S of San José, 1900 m, *Williams 19450* (US); cloud forest area, slopes of Cordillera de Talamanca, *Williams, Jiménez & Williams 24333* (CR, F, US); Talamanca, *Williams 28597* (F, NY, US). PANAMA. Chiriquí: "New Switzerland", central valley of Río Chiriquí Viejo, 1800-2000 m, *Allen 1349* (F, GH, MO, NY, US); E facing slope above Cerro Horqueta, 1660-1700 m, *Cochrane, Cochrane & Kowal 6242* (MO, WIS); between Bambito and Cerro Punta, *Croat 10566* (MO); N of Audubon cabin, *Croat 13629* (MO); above San Felix along mining rd 18-27 mi off Panamerican Hwy, 1200-1500 m, *Croat 33075* (MO); Cerro Punta, 0.5 mi SE of Entre Ríos, 1 mi by road from Cerro Punta, 2000 m, *Croat 48577* (MO); Bajo Chorro, Boquete District, 6000 ft, *Davidson 108* (F, GH, MO, US); oak forest, Río Piedras Candella, 1800 m, *McAlpin 2200* (DUKE); humid oak-laurel forest near Río Chiriquí Viejo 1.5 mi W of Cerro Punta, 1700 m, *MacDaniel 10126* (DUKE); Bajo Grande, 1-3 km E of Cerro Punta, 2000-2200 m, *Nee 9980* (MO); high forest along Quiel rd 10 km above Boquete, 5500 ft, *Proctor 31802* (LL); W slope of El Barú, 7000-8000 ft, *Tyson & Loftin 5968* (US); W of Cerro Punta near Las Nubes, 6100-6400 ft, *Utley 5657* (CAS, DUKE, MO, NY, US); hillside above rd along Río Chiriquí Viejo, *Utley 5687* (B, BR, C, DUKE, F, G, GH, MEXU, MICH, MO, NY, TEX, US, WIS); *White & White* (F, MO, VT); wooded slopes about 1 km N of Las Nubes, 2000-2300 m, *Wilbur et al. 15250* (DUKE).

6. *Begonia garagarana* C.DC., Smithson. Misc. Coll. 69: 2. 1919. TYPE: PANAMA: Cerro de Garagará, Sambú Basin, southern Darién, 500-940 m, February 7, 1912, *Pittier 5672* (Holotype: US!).

Terrestrial herbs; *rhizomes* repent, 10-57 cm long; internodes elongate, 0.9-5.5 X 0.5-1.3 cm, puberulous when young, with spreading or adpressed trichomes 0.1-1 mm long, intermixed with minute glandular trichomes, glabrescent with age. *Leaf blades* simple, chartaceous, oblique, usually asymmetrically suborbicular or rarely broadly oblong, 16-26 X 11-20 cm, basally narrowly deeply cordate or occasionally broadly shallowly cordate, apically abruptly short acuminate, marginally irregularly crenulate to denticulate, glabrous throughout above but glandular in intercostal regions and glandular-puberulous on nerves beneath, palmately 11-13-nerved. *Petioles* 13-40 cm X 0.5-5 mm, sparsely pubescent when mature with minute glandular trichomes intermixed with the antrorsely adpressed 0.1-1 mm trichomes. *Stipules* caducous, chartaceous, asymmetrically oblong to lanceolate, 1.7-3.4 X 0.5-0.9 cm, weakly to strongly keeled, apically acute, marginally entire, glabrous or the costa only fimbriate. *Inflorescences* typically exceeding the leaves, cymes asymmetric to unilateral, few- to many-flowered, 7-14 cm diam. *Peduncles* 39-81.5 cm X 1-6 mm, sparsely puberulous with trichomes spreading to antrorse, but glabrate with age. *Bracts* caducous, the lowermost navicular, broadly obovate, 1.4-1.9 X 1-1.6 cm, weakly keeled distally, apically acute to obtuse, marginally entire, glabrous. *Staminate flowers*: pedicels 1.2-1.5 (4) cm long; sepals suborbicular to broadly oblong, 0.9-1.5 X 0.8-1.6 cm, glabrous; petals wanting or 2, narrowly obovate-oblanceolate, 6.5-10 X 3-4 mm; stamens 30-46; filaments 0.1-1 mm long, inserted on a low torus; anthers narrowly oblong to obovate, 2-2.8 X 0.4-0.8 mm. *Pistillate flowers*: pedicels 1 cm long; bracteoles wanting; sepals suborbicular, 0.9-1 X 0.9-1 cm, glabrous; petals wanting, 1 or 2, oblanceolate, 4 X 2 mm; ovaries 4-4.5 mm long; styles 3, connate briefly basally; stigmas bicornute. *Capsules* with pedicels 1.7-3 cm long, trilocular, 4-8 mm long; locule chambers externally appearing ovate or cordate, 3-6 X 4-7.5 mm; wings 3, unequal, the largest asymmetrically dolabriform to ovate or elliptic, (1.4) 2-2.8 X (0.7) 1.1-1.5 cm, apically rounded to broadly ovate, the second and third asymmetrically triangular, marginiform.

DISTRIBUTION AND HABITAT: Endemic to Panama ranging from the vicinity of Santa Fé in Veraguas Province to Cerro Pirre in the Darién at elevations between 450-1400 m on wet forested slopes (Fig. 11).

FLOWERING: Flowering specimens have been collected between December and April.

DISCUSSION: *Begonia garagarana* is poorly collected and available specimens lack sufficient floral material to provide adequate information on variability in floral characters. Although poorly known, *B. garagarana* stands apart from other species in sect. *Gireoudia* with its caulescent rhizomatous habit, elongate internodes, caducous, oblong to lanceolate stipules and sparingly puberulent indument.

With its elongate, puberulous internodes and bicornute stigmas, *Begonia garagarana* is similar to the suffrutescent species but differs from these species in its rhizomatous habit, asymmetric to unilateral inflorescences and unusual vertically ridged or sinuate placentae. The only other rhizomatous species with bicornute stigmas in the section are *B. urophylla, B. louis-williamsii, B. croatii, B. nelumbiifolia* and *B. fusca. Begonia garagarana* differs from the first four taxa in its very sparse indument of villi, elongate internodes, generally larger sepals, small capsules with large primary wings and its unusual ridged placentae. Only one other species in sect. *Gireoudia* in Central America has strongly ridged placentae, *B. fusca,* with which *B. garagarana* also shares similar villi, often caducous stipules, pistillate and staminate flowers occasionally with petals and often dolabriform capsule wings. *Begonia garagarana* differs from *B. fusca* in its more sparse indument, puberulous internodes, smaller leaves, membranaceous sepals, fewer stamens and smaller capsules.

SPECIMENS EXAMINED: PANAMA. Darién: Pirre, *Bristan 465* (MO); *Duke 6577* (MO); *Gentry & Clewell 6953* (DUKE, MO). Veraguas: forested slopes of Cerro Tute, vicinity of Santa Fé, 2500 ft, *Allen 4375* (in part) (MO); near Escuela Agrícola Alto Piedra near trail to top of Cerro Tute, 2200-2400 ft, *Antonio 3534* (MO); stream in valley of Río Dos Bocas NW of Santa Fé, 450-550 m, *Mori et al. 3812* (MO); Pacific slopes above stream NW of Santa Fé, Alto de Piedra, *Mori et al. 3953* (MO).

Fig. 11. Distribution of *Begonia croatii* (squares), *B. garagarana* (circles) and *B. morii* (triangles).

7. *Begonia fusca* Liebm., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1852: 7. 1852. TYPE: MEXICO: Oaxaca: S. Jago Amatlán, 4500 ft, July 1842, *Liebmann s.n.* (Lectotype: C!; isolectotype: C!).

   Magnusia maxima Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854. *nom. nud.*

   Magnusia fusca (Liebm.) Kl., Abh. Königl. Akad. Wiss. Berlin 1854: 222. 1855.

   Magnusia maxima Kl., Abh. Königl. Akad. Wiss. Berlin 1854: 223. 1855. TYPE: MEXICO: Hort. Bot. Berol. July 1853. (Holotype: B!).

Herbaceous perennials; *rhizomes* repent; internodes 1.5-3 X 1.2-3.5 cm, lenticellate, densely squamose, the fimbriate-lacerate scales 0.3-1.6 cm long. *Leaf blades* simple, oblique, asymmetric, suborbicular or broadly elliptic to ovate or obovate, 18-48 (90) X 13.5-35 cm, basally narrowly to broadly deeply cordate, with lobes frequently overlapping, apically acuminate to attenuate-acuminate, marginally irregularly dentate, ciliate-denticulate and ciliate, sparsely to moderately hirsute above and beneath but more dense on principal nerves below, palmately 10-12-nerved. *Petioles* 26.5-72 (150) cm X 4-13 mm, moderately to densely hirsute when immature, the spreading to matted villi 0.5-2 mm long, frequently with glandular trichomes intermixed. *Stipules* caducous to semipersistent, subcoriaceous, asymmetrically ovate, 1-2 X 0.8-2 cm, strongly keeled, apically acute, marginally entire, glabrous or hirsute throughout, but only the keel strongly lacerate-fimbriate. *Inflorescences* potentially exceeding the foliage, symmetric to weakly asymmetric, laxly cymose, many-flowered, 15-30 cm diam. *Peduncles* 33-84 X 0.6-1.5 cm, moderately to densely hirsute or tomentose when immature, with minute glandular trichomes frequently intermixed, but glabrate with age. *Bracts* caducous, navicular, asymmetric, ovate to elliptic, 3.1-4.5 X 1.3-2.4 cm, weakly keeled, apically acute to subacuminate, marginally ciliate-serrulate, this especially pronounced from midlamina to apex; densely hirsute throughout with occasional lacerate-fimbriate scales and minute glandular trichomes. *Staminate flowers*: pedicels 0.8-1.3 (2.3) cm long; sepals subcoriaceous, white to pink, broadly elliptic to suborbicular or ovate, 1-2 X 1-1.9 cm, externally sparsely pilose medially; petals generally wanting, but when present, 2, chartaceous, narrowly obovate, 6 X 4 mm; stamens 50-82; filaments 0.8-2 mm long, inserted on a slightly raised torus; anthers narrowly oblong, obovate or oblanceolate, 1.9-3.1 X 0.5-1 mm. *Pistillate flowers*: pedicels 0.5-2 cm long; bracteoles wanting; sepals subcoriaceous, colored like the staminate sepals, suborbicular 0.9-1.8 X 0.9-1.6 cm, sparsely pilose to glandular pilose medially; petals generally wanting, but when present, 1, elliptic to narrowly obovate, 7-8 X 3.5 mm; ovary 6-10 mm long, sparingly pilose or glandular-pilose throughout, margins of wings commonly ciliate; styles 3, 2-3 mm long, connate to 1/2 their length; stigmas bicornute. *Capsules* with pedicels (2.2) 2.5-4.4 (5.5) cm long, trilocular, 0.9-1.5 (1.9) cm long, with strongly vertically ridged or sinuate bipartite placentae; locule chambers appearing oblong to weakly ovate, 8-13 X 7-22 mm wide; wings 3, unequal, marginally ciliate, the largest variable in form, asymmetric, ovate, obovate, dolabriform or occasionally elliptic, 1.6-3.8 X 1.4-2.8 cm, the second asymmetrically lunate to broadly but shallowly triangular, 0.7-1.2 (1.5) X 0.9-1.4 (1.7) cm, the third margini-

form and very shallowly lunate.

DISTRIBUTION AND HABITAT: Southern Mexico, Guatemala and Honduras between 1000-3000 m elevation (Fig. 12).

FLOWERING: Flowering material of *B. fusca* has been collected throughout the year.

DISCUSSION: *Begonia fusca* is perhaps the largest species in sect. *Gireoudia* with leaf blades to 90 cm long and petioles to 150 cm long. Although *B. fusca* attains these dimensions, the vast majority of preserved specimens contain plant parts significantly smaller or lack major plant parts including rhizomes, petioles and peduncles. Because size variation was determined from these specimens, it is not necessarily an accurate measure of the upper size limits of many characters of *B. fusca*.

I chose as the lectotype of *B. fusca* a specimen of *Liebmann s.n.* at Copenhagen which was gathered near S. Jago Amatlán in Oaxaca, Mexico. One of the other collections cited by Liebmann (1852), Tonaguia, Mexico contained leaves of a still undetermined taxon.

Begonia fusca is readily determined by its large, pilose subcoriaceous sepals, numerous stamens, strongly vertically ridged or sinuate placentae, large capsules and capsule wings with ciliate margins. Like several other species in the section, both staminate and pistillate flowers occasionally have petals.

In his treatment of the Begoniaceae, Klotzsch (1855) described *B. maxima* from cultivated material available at Berlin. While he included *M. fusca* as a distinct species within *Magnusia*, following his description of *M. maxima*, Klotzsch listed his illustration of *M. fusca*. Since there are no apparent differences between these taxa, it is unclear whether Klotzsch was placing *M. fusca* in synonymy with *M. maxima* or whether this was a typesetter's error.

With its villous indument and bicornute stigmas, *B. fusca* resembles several rhizomatous taxa. Among the rhizomatous taxa with villous induments and bicornute stigmas, only *B. garagarana*, a Panamanian endemic, regularly has staminate and pistillate flowers with petals and similar placentae. The salient

Fig. 12. Distribution of *Begonia fusca* (triangles), *B. pinetorum* (circles) and *B. thiemei* (squares).

features which distinguish these taxa are presented in the discussion of *B. garagarana*.

SPECIMENS EXAMINED: MEXICO. Chiapas: near Puerto del Viento, 9 m N of Pueblo Nuevo Solistahuacán, Municipio of Rayon, 6100 ft, *Breedlove 10156* (DS, F, MICH); wooded ridge 7 mi N of Jitotol on side road to an oil-well, Municipio of Jitotol, 6700 ft, *Breedlove 15395* (DS, F, MICH, US); Summit of Chuchil Ton, NE of Bochil, Municipio of San Andrés Larrainzar, 2700 m, *Breedlove 6847* (DS, MEXU, MICH, MO); *Breedlove 29264* (DS); *Breedlove 34664* (DS); E base of Cerro Tres Picos near Cerro Bola along logging road SW of Colonia Agrónomos Mexicanos, Municipio of Villa Corzo, 1500 m, *Breedlove & Thorne 30172* (DS); ridge above Siltepec on road to Huixtla, Municipio of Siltepec, 2000-2400 m, *Breedlove & Smith 32001* (DS, MEXU, MICH, MO); *Breedlove 40412* (DS); Selva Negra 10 km above Rayon Mezcalapa, Municipio of Rayon, 1700 m, *Breedlove & Smith 32591* (DS); ridge above Jitotol, Municipio of Jitotol, 6500 ft, *Clark 176* (DS); Hwy 195 between Bochil and Pichucalco, steep slopes below lookout, 1900-1950 m, *Croat 46368* (MO); rd between Motozintla de Mendoza and Siltepec, 26-30 mi N of Motozintla, 1000-1300 m, *Croat 47441* (MO); Hwy 195 between Ixtapa and Pichucalco ca 1 mi below lookout, *Croat 47808* (MO); Mt. Ovando, Escuintla, *Matuda 4210* (GH, MEXU, MICH); Tres Cruces, Sierra Madre, 2600 m, *Matuda 5019* (F); Siltepec, Motozintla, 2100 m, *Matuda 38523* (DS, MEXU); ridge above Pueblo Nuevo Solistahuacán, Municipio of Pueblo Nuevo Solistahuacán, 6500 ft, *Shilom Ton 2874* (DS, F, MICH); *Tillett 636-62* (GH). Oaxaca: Trapiche de la Concepción, 3000 ft, *Liebmann s.n.* (B); Tonaguia, 5000 ft, *Liebmann s.n.* (C pro parte). Puebla: Apulco, 1400 m, *Boege 1226* (MEXU); *Boege 1348* (MEXU); *Boege 2351* (MEXU); Cascades of Río Frio near km 350 on rd below Teziutlán, 1400 m, *Moore & O'Gorman 6292* (BH). Veracruz: Environs d'Orizaba. S. Cristóbal, *Botteri & Sumichrast 1631* (P); valle de Córdova, *Bourgeau s.n.* (P, US); Cerro San Cristóbal, Orizaba, *Miranda 4854* (MEXU); Agua Santa cerca de Ocotepec. Municipio de Jalacingo, 1750 m, *Ventura 289* (MICH). GUATEMALA. Alta Verapaz: road to Cobán N of Salama beyond Kilila, Sierra de las Minas, *Clover 9625* (MICH); road to El Estor (Lago Izabal) 2 mi E of Hwy, 1300 m, *Croat 41443* (MO); Cobán, *Johnston 1152* (F); Tactic, 1480 m, *Standley 71219* (F); mountains E of Tactic on road to Tamahú, 1500-1650 m, *Standley 71299* (F); *Standley 90556* (F); *Standley 90574* (F); *Standley 91514* (F); wet forest near Tactic, 1400-1500 m, *Standley 90460* (F); Tactic-Cobán, *von Tuerckheim II 2040* (GH, US); Río Cobán about 5 km SE of Tactic, 1300-1500 m, *Williams et al. 40605* (F). Baja Verapaz: N of divide N of Santa Rosa, 1650 m, *Standley 69879* (F). Quiché: valley of Río de las Violetas, N of Nebaj, 5800-6000 ft, *Proctor 25259* (DS, LL). Huehuetenango: without further locality, 7000 ft, *Skutch 1122* (GH); Cerro Negro, 2 mi W of Las Palmas, Sierra de los Cuchumatanes, 1600-2000 m, *Steyermark 51734* (F, GH); *Steyermark 51735* (F, GH). Quetzaltenango: above Mujulia, between San Martín Chile Verde and Colomba, 1500 m, *Standley 85530* (F); *Standley 85699* (F); Río Salama, between Santa María de Jesús and Calahuaché, 1200-1300 m, *Steyermark 33876* (F, US). San Marcos: between San Rafael at NE portion of Volcán Tacaná and Guatemala-Mexico line, 2500-3000 m, *Steyermark 36346* (F). Zacapa: pine-covered canyon bordering Río Lima, Sierra de las Minas, below Alejandrai, 2000 m, *Steyermark 30027* (F). HONDURAS: Ocotepeque: Belen Gualcho y alrededores 40 km E of Nueva Ocotepeque, 1500-2000 m, *Nelson et al. 3791* (MO).

8. *Begonia urophylla* Hook., Bot. Mag. 81: t. 4855. 1855. TYPE: Described from cultivated material sent from Brussels Botanical Garden to Kew (Holotype: K!).

   Gireoudia setosa Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854. *nom. nud.*

   Gireoudia urophylla (Hook.) Kl., Abh. Königl. Akad. Wiss. Berlin 1854: 212. 1855.

   Gireoudia setosa Kl., Abh. Königl. Akad. Wiss. Berlin 1854: 212. 1855. TYPE: CENTRAL AMERICA: Chiriquí: cultivated from seed sent to Berlin, *Warscewicz 1756* (Holotype: B!); non *Begonia setosa* Kl.

   Begonia setifera A.DC., Prodr. 15(1): 338: 1864. Substitute name for *G. setosa* Kl.

   Begonia squamosa C.DC., Bull. Herb. Boiss. II. 5: 315. 1908. TYPE: COSTA RICA: Cañas Gordas, 1100 m, February 1897, *Pittier 11181* (Holotype: BR!; isotypes: BR!, CR!, US!).

   Begonia villipetiola C.DC., Smith-

son. Misc. Coll. 69: 5. 1919. TYPE: PANAMA: Bismarck above Penonome, 2000-3000 ft, March 5-19, 1908, *Williams 309* (Holotype: US!; isotype: NY!).

Begonia stigmosa sensu Smith & Schubert, Caldasia 4: 14. 1946. *et seqq.*

Begonia santae-martae Irmsch., Bot. Jahrb. 74: 618-619. 1949. TYPE: COLOMBIA: Santa Marta, 4000 ft, December 1898-1901. *Smith 1262* (Lectotype: B!; isolectotypes: BR!, GH, MO!, NY! [2 sheets)], US!).

Begonia boquetensis Irmsch., Bot. Jahrb. 78: 179-180. 1959. TYPE: PANAMA: Veraguas, Boquete, *Seemann 1659* (Holotype: K!; isotype: BM!).

Acaulescent herbs; *rhizomes* repent, unbranched when young but often branching with age, 4-21 cm long; internodes 0.2-1.6 X (0.2) 0.5-2.5 cm, strongly lenticellate, moderately to densely squamose or squamose-villous with narrow entire or broad lacerate translucent white scales 2-6 mm long but becoming glabrate in age; nodes often with a conspicuous band of scales surrounding the petiole base or leaf scar. *Leaf blades* simple, chartaceous to subcoriaceous, oblique to transverse, asymmetric, suborbicular, broadly to narrowly ovate, oblong-elliptic or rarely obovate, (8.1) 10.4-29.3 X (4.3) 6-16.5 (19.7) cm, basally narrowly or broadly shallowly to deeply cordate with lobes only rarely overlapping, apically attenuate-acuminate or infrequently abruptly short acuminate, marginally ciliate and ciliate-denticulate to ciliate-serrulate and dentate or serrate opposite ends of major nerves, commonly with a conspicuous cusp on the side of the blade opposite the petiole insertion, upper leaf surface dark green, scabrous to hirsute throughout, only rarely glabrous, nitidous and lower leaf surface with principal nerves sparsely to moderately villous or squamose, but when squamose, the broad lacerate-laciniate scales confined to principal nerves and intercostal regions glabrous, and if villous, the narrow entire scales confined to principal nerves or villous throughout, occasionally glandular throughout, palmately (8) 9-11 (12)-nerved. *Petioles* light green to green deeply suffused with red, (6.5) 11-30.5 (52) cm X 1.5-3 (8) mm, strongly lenticellate, either moderately to densely squamose or squamose-villous throughout with spreading to reflexed broadly laciniate-lacerate scales 2-6 mm long X (0.3) 1-3 mm wide or narrow, entire scales (1.5) 3.5-5 mm long X 0.1-0.3 mm wide. *Stipules* persistent to subpersistent, often disintegrating with age, commonly translucent red but brunneous when dry, asymmetrically narrowly to broadly ovate-triangular or ovate, 0.9-1.7 X 0.6-1.1 (1.2) cm, strongly keeled with the keel excurrent apically or subapically, marginally entire, densely villous or squamose-villous throughout or the lamina glabrous to glandular throughout, but the keel strongly laciniate-fimbriate especially basally. *Inflorescences* often greatly exceeding the foliage, symmetric to weakly or moderately asymmetric, frequently densely cymose when immature but often becoming laxly so in age, many-flowered, (4.6) 7-25 cm diam. *Peduncles* light green to red, (8) 24-80 X 0.2-1.2 cm, sparingly villous to squamose-villous, often with glandular trichomes intermixed. *Bracts* caducous, often deep pink to red, the lowermost often navicular, suborbicular, broadly oblong-elliptic or subobovate, (6) 11-15 (25) X (4.5) 6-9 (11) mm, keeled, apically obtuse or mucronate, marginally ciliate-denticulate, moderately to densely villous or glandular-villous. *Staminate*

flowers: pedicels (6) 8-13 (17) mm long; sepals white to pale pink, broadly ovate, obovate, elliptic or suborbicular, (8) 11-15 X (6.5) 10-14.5 mm, apically rounded to acute; petals typically wanting, but if present, commonly 1 or rarely 2, white, obovate, 6-9 X 1-3 (4.5) mm; stamens (23) 33-61; filaments 0.7-2.5 (3) mm long, occasionally borne on a low torus; anthers oblong-obovate, (0.7) 0.8-1.2 X 0.3-0.7 mm. *Pistillate flowers*: pedicels (3.5) 5-18 (22) mm long; bracteoles wanting; sepals colored like staminate sepals, suborbicular, broadly ovate or transversely elliptic, (4) 6-10 (13) X (4.5) 6.5-12 (14.5) mm, sparingly glandular throughout or less frequently glabrous; petals typically wanting, rarely 1, oblanceolate to subelliptic-obovate, 4-9 X 1-4.5 mm; ovary (3.5) 4-6.5 mm long, glabrous or glandular throughout; styles 3, 1-1.5 mm long, connate to 1/2 their length; stigmas bicornute. *Capsules* with pedicels (8) 14-22 (37) mm long, trilocular, (6) 7-10 mm long; locules externally appearing suborbicular, broadly elliptic, ovate or obovate, (3.5) 5-6 (7.5) X 4-6 mm; wings 3, unequal, the largest asymmetric or rarely symmetric, narrowly ovate-triangular to broadly ovate, oblong-elliptic or suborbicular, (9) 12-18 (26) X (6.5) 8.5-10 (16) mm, apically obtuse or infrequently acute, the second asymmetrically ovate to broadly triangular or lunate, (4) 5-9 X (6) 7-9 (11) mm, the third broadly, shallowly lunate or often marginiform, (4) 5-7.5 X 6-9 mm.

DISTRIBUTION AND HABITAT: *Begonia urophylla* extends from Guatemala to Colombia and Venezuela. No collections are presently known from Nicaragua and Honduras, but *B. urophylla* has been collected from lower elevations in northern Costa Rica. *Begonia urophylla* inhabits wet forested areas from sea level-2000 m, frequently growing on steep forested slopes where it forms small isolated colonies, but it may also become established on open roadbanks (Fig. 13).

FLOWERING: Flowering is profuse from late November to April.

DISCUSSION: In the Flora of Colombia and later in the Floras of Panama and Guatemala, Smith and Schubert (1946b, 1958, 1961) treated the specimens now recognized as *B. urophylla* as *B. stigmosa*, a species they considered wide ranging, extending from Mexico to northern South America. As *B. stigmosa* is presently understood, it is restricted to the Mexican states north of Chiapas, while *B. urophylla* ranges from Central America to northern South America. *Begonia urophylla* differs from *B. stigmosa* in several subtle but significant floral characters including stamen number which ranges from 23 to 61 in *B. urophylla* versus 6-19 in *B. stigmosa* and its bicornute stigmas which are a marked contrast to the lunate stigmas observed on *B. stigmosa*. With leaves of similar size, shape and indument, these two species are almost indistinguishable vegetatively. Excluding some Panamanian and Costa Rican populations of *B. urophylla* with villous-squamose petioles, both species have squamose petioles but occasionally differ in blade margination; many specimens of *B. stigmosa* have irregularly shallowly lobed leaves without a conspicuous secondary cusp opposite the petiole insertion, while leaves of *B. urophylla* are unlobed except for an occasional conspicuous secondary cusp. The adaxial leaf surfaces of these species often differ, with those of *B. urophylla* being generally scabrous or hirsute and only rarely glabrous, but with those of *B. stigmosa* being glabrous or sparingly glandular throughout.

Irmscher (1959), recognizing the significant floral differences between *B. stig-*

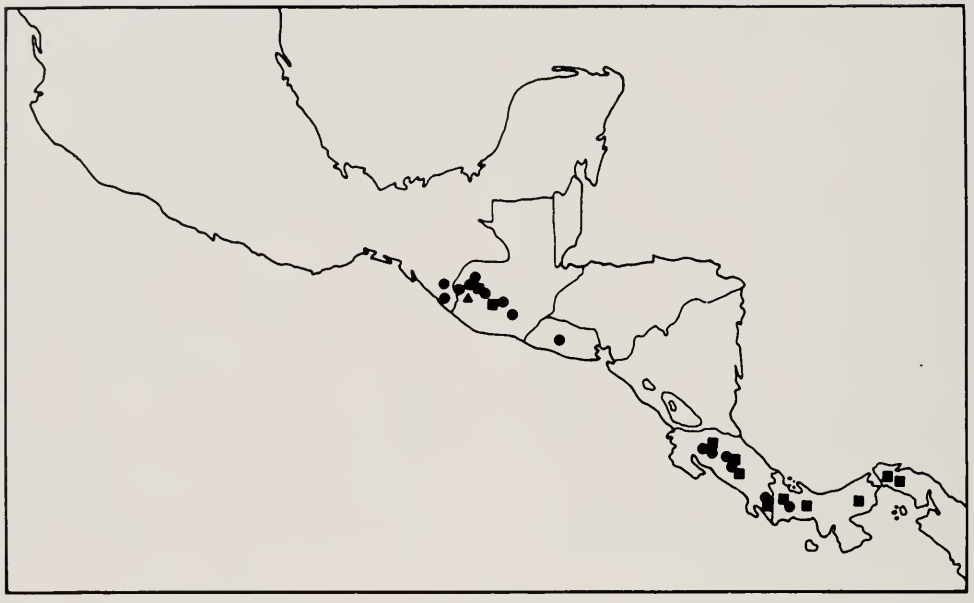

Fig. 13. Distribution of *Begonia louis-williamsii* (triangles), *B. strigillosa* (circles) and *B. urophylla* (squares).

mosa and *Seemann 1659* which Candolle (1864) mistakenly included in *B. stigmosa*, described *B. boquetensis*, apparently unaware of *B. urophylla* and several other earlier epithets applied to this taxon. Although he discussed the relationship between *B. santae-martae* and *B. stigmosa* (Irmscher, 1949), Irmscher overlooked the potential relationship between the former taxon and *B. boquetensis* in this later paper. *Begonia santae-martae* was most recently treated as a synonym of *B. stigmosa* sensu Smith & Schubert in the Begoniaceae of Venezuela (Smith, 1973).

Begonia squamosa and *B. villipetiola* which are here included in *B. urophylla* represent the extremes in petiolar vestiture encountered in *B. urophylla*. Petioles on the type of collection of *B. squamosa* from near Cañas Gordas, Costa Rica, are densely squamose with broad lacerate scales to 4 mm wide, while the petiolar indument on the type of *B. villipetiola* consists of very narrow (less than 0.5 mm wide basally) entire to infrequently lacerate scales. Many specimens including the types of *B. urophylla* and *Gireoudia setoka* are intermediate in this character with scales broader than those observed on the type of *B. villipetiola* but much narrower than scales on *B. squamosa*. Individuals with narrower scales frequently occur at lower elevations than broad scaled plants and have modal values for peduncle length, sepal length and pedicel length slightly lower than those observed in the broad scaled specimens, but there is a broad overlap in these largely morphometric characters. In stamen number, anther size and shape, stigma form and capsular characters, the forms are indistinguishable and are best treated as part of a single variable species.

Begonia urophylla belongs to the urophylla species group which includes *B. croatii* and *B. quaternata*. The relationships among species in this group are discussed under the latter two taxa. While *B. urophylla* differs markedly

from *B. louis-williamsii* in the strigillosa species group, these taxa overlap in many morphometric characters and frequently have similar blade and petiolar indu-ments. They also share bicornute stigmas which are uncommon among the rhizomatous taxa in sect. *Gireoudia,* but which are characteristic of all but one of the suffrutescent species. *Begonia urophylla* differs from *B. louis-williamsii* in its generally larger size, somewhat broader leaf blades, more numerous flowers per inflorescence, smaller sepals, more numerous stamens and primary wing form.

Begonia urophylla is potentially sympatric with a number of species in sect. *Gireoudia,* and has been collected growing intermixed with *B. sericoneura* in a recently disturbed area in Alajuela Province, Costa Rica (*Utley 5933*). Within the same population were several morphological intermediates (*Utley 5931, Utley 5927*) between *B. sericoneura* and *B. urophylla* which produced no viable pollen.

SPECIMENS EXAMINED. GUATEMALA. Alta Verapaz: between Tactic and Cobán, *von Türckheim II 2040* (NY); Chimaltenango: wet thicket near Yepocapa, 1350 m, *Standley 62325* (F). Quetzaltenango: steep slopes in forest, Colomba, *Skutch 2016* (GH); near El Muro below Santa María de Jesús, 120 m, *Standley 67216* (F); damp forest, Finca Azucena above Colomba, 1320 m, *Standley 68098* (F); Finca Pirineos below Santa María de Jesús, 1350-1380 m, *Standley 68436* (F); lower S facing slopes of Volcán Santa María between Santa María de Jesús and Calahuaché, 1300-1600 m, *Steyermark 33274* (F). Retalhuleu: Rio Samala, 1700 ft, *Smith 1469* (US); E of Chivolandia, 1020 m, *Standley 67024* (F); *Standley 67049* (F); near Chivolandia along rd to San Filipe, 650 m, *Standley 87189* (F, GH). San Marcos: steep rocky cliffs, Finca Armenia near La Trinidad, *Croat 47089* (MO); wet thicket, Río Ixpal, below Roadeo, 750 m, *Standley 68747* (F); lower S facing slopes of Volcán Tajumulco between Finca El Porvenir to "Numero 6", 1300-1500 m, *Steyermark 37112* (F); Suchitepéquez: SW slopes of Volcán Zunil in vicinity of Finca Montecristo, 1200-1300 m, *Steyermark 35205* (F). Without further locality: *Rodriguez 162* (P); *Rodriguez 530* (P). COSTA RICA. Alajuela: San Pedro de San Ramón, 1050 m, *Brenes 5380* (CR [in part], F); *Brenes 6582* (F); *Brenes 15083* (CR, F); "Alto de la Calera" de San Ramón, *Brenes 5894* (CR, F); Cataratas de San Ramón, *Brenes 13522* (F); *Brenes 13537* (CR); entre Río Jesús y Calera de San Ramón, *Brenes 17067* (CR, F, NY); near La Laguna, 6-8 km S of Villa Quesada, 1200 m, *Molina et al. 17549* (F): San Juan de Lajas cloud forest, Canton San Carlos, 1400 m, *Smith 1480* (GH, NY); Caribbean rain forest, Sucre, San Carlos, 1025 m, *Smith 11673* (F); 4 km S of Bajo Rodriguez on rd between San Ramón and Bajo Rodriguez, *Utley & Utley 4622* (CR, DUKE, US); disturbed primary forest 4-5 km N of Bijagua, 500-600 m, *Utley 5926* (DUKE). Cartago: secondary vegetation between Navarro and Muñeco, *Utley 5880* (CAS, CR, DUKE, K, MEXU, MO, NY, US). Guanacaste: evergreen cloud forest on E slopes of Volcán Miravalles (Cerro La Gigante), 800 m, *Burger & Gentry 9102* (CR, F, MO). Puntarenas: forest bordering airstrip, GROMACO, Buenos Aires, 1100 ft, *Arnold 1* (CR); *Arnold 7* (CR); roadside vegetation between Agua Buena and escarpment above Villa Neilly, 1000 m, *Burger & Mata 4588* (CR, F); primary forest along Río Coto Brus, near Coton, *Croat 26612A* (MO); Terraba, *Leon 1126* (CR); lower slopes of Cordillera de Talamanca on property of Compania Las Alturas, *Utley & Utley 4813* (DUKE). San José: El General, 1130 m, *Skutch 3008* (GH, MO, NY, US). PANAMA. Bocas del Toro: Río Terebe just below Puerto Palenque, 350 ft, *Kirkbride & Duke 552* (MO). Canal Zone: Mojinga Swamp near mouth of Río Chagres, 1 m, *Allen 864* (BR, F, MO, NY); forest along banks of Quebrada La Palma and Cañon of Río Chagres, 70-80 m, *Dodge & Allen 17368* (MO); limestone rocks in forest in NW part of Canal Zone, divide between Río Piña and Río Media, *Johnston 1821* (A, MO); secondary forest along rd S-1 between Gatún and Piña, 0-170 m, *Liesner 1352* (F, MO); hills W of Canal near Gatún, *Standley 27204* (US). Chiriquí: rocky slope 12 mi from Gualaca on rd to Cerro Hornito, 1300 m, *Antonio 1748* (MO); Hwy 11, 0.5 km W of Quebrada La Cruzo Coloradito, 2.5 km W (by air) of Cerro Pando, 1240 m, *Cochrane, Cochrane & Kowal 6295* (WIS); *Cochrane, Cochrane & Kowal 6303* (MO); Palo Santo, 3 mi N of Volcán, *Croat 13567* (F, MO, NY); *Croat 13571* (MO); highway west of Cerro Pando, 600 ft, *D'Arcy & D'Arcy 6653* (DUKE, MO); 5 km S of Volcán on rd to David, 600-750 m, *Graham 267* (GH, MICH); Boquete, *Lewis et al. 382* (GH, MO, US); *Maxon 4947* (NY, US); *Pittier 2896* (US); eastern Chiriquí between Hato de Jobo and Cerro Vaca, 700-1000 m, *Pittier 5411* (US); Sta. Clara cerca de Cerro Pando en la frontera con Costa Rica, *Troetsch 46* (MO).

Coclé: El Valle, 800-1000 m, *Allen 213* (MO); *Allen 238* (MO); *Allen 1184* (MO); *Allen 1664* (F, GH, MO, NY, US); *Allen 2906* (GH, MO); *Allen 4216* (MO); 2 mi above El Valle, rd to La Mesa, *Croat 13305* (F, MO); La Mesa, 600-800 m, *Duke & Dwyer 15171* (NY); Margarita, near chicken farm, *Dwyer & Lallathin 8281* (MO); rd back of Club Campestre, El Valle, *Dwyer 11848* (MO); 1 mi N of El Valle, *Gentry & Dwyer 3577* (F, MO); 29 km N Penonome on rd to Coclesito, 500 ft, *Hammel 1712* (MO); El Cope on slope and ridge W of sawmill, *Hammel 2418* (MO); 2 mi N of Cerro Pilon, 900 m, *Liesner 740* (F, MO, NY). Darién: premontane wet forest well below summit, S slope of Cerro Tacarcuna, 1250-1450 m, *Gentry & Mori 13933* (MO). Panamá: dirt road to Cerro Campana, *Correa & Dressler 834* (DUKE, MO); *Correa & Dressler 846* (MO); *Croat 12059* (MO); La Eneida, region of Cerro Jefe, *Dressler 4282* (DUKE, F, MO); Rancho Chorro, mts above Torti Arriba, Canazas mountain chain, *Folsom, Collins & Alonzo de Monte 6730* (MO); Cerro Campana above Su Lin Motel, *Porter et al. 4156* (MO); *Porter et al. 4192* (MO, UC); 800 m, *Utley 5708* (B, BR, C, CGE, DUKE, F, GH, MICH, MO, NY, US). San Blas: seasonal evergreen forest along river, headwaters of Rio Cuadi, Camp Diablo, *Duke, Robyns & Verhoek 3631* (MO). COLOMBIA. Boyacá: Cordillera Oriental, vertiente orienta, Municipio de Tauramena, vereda de Malpaso, 1300-1400 m, *Uribe Uribe 3928* (US); la carretera de Casanare entre Corinto y el Salto de Candelas, 1750 m, *Uribe Uribe 6427* (US). Guajira: region del Campano, Sierra Nevada de Santa Marta, 1300 m, *Barkley & Gutierrez 1893* (US); Sierra Nevada de Santa Marta entre Riohacha y Pueblo Viejo, 700 m, *Barclay & Juajibioy 6859* (US). Magdalena: stream above Manaure, 800 m, *Haught 3953* (US); Sierra Nevada de Santa Marta above Minca between Vista-Nieve and Los Cumbres, 1500 m, *Hawkes 595* (US); Sierra Nevada de Santa Marta, Bergwald oberhalg Cincinnati, 1200-1600 m, *Schultze 469* (B); Cincinnati, lower slopes of Mount San Lorenzo, near Santa Marta, 1300 m, *Seifriz 56* (US); Vista Nieve, Santa Marta, *Viereck 8* (US). Meta: mts of Cordillera Oriental near Villavicencio, 800 m, *Epple 372* (US); Cordillera La Macarena, entre el Río Güejar y el caño Guapayita, 500-600 m, *Idrobo & Schultes 835* (US). Norte de Santander: Cordillera Oriental, Sarare, hoya del Río Margua entre Junin y Córdoba, 920-1240 m, *Cuatrecasas 13375* (US). VENEZUELA. Lara: Distrito Jiménez, Paso de Angostura, sitio de represa Yacambú, 500 m, *Steyermark & Carreno Espinosa 108743* (US). Merida: Filo del Sai-Sai, El Carrizal, 1850 m, *Bernardi 2073* (NY); Distrito Libertador, Río Los Micuyes, 1450 m, *Ruiz-Terán & Lopez-Figueiras 10541* (US); rich woodlands between La Azulita and La Carbonera, *Steyermark 56068* (NY, US). Zulia: Perijá, 1175 m, *Gines 1472* (US); *Gines 1856* (US); Sierra de Perijá cerca la frontera Colombo-Venezolana, 1440 m, *Steyermark & Dunsterville 105594* (US). State unknown: Santo Domingo, 2500 m, *Bogner 776* (M).

9. *Begonia croatii* Burt-Utley, Brittonia 34: 196. 1982. TYPE: PANAMA: Veraguas: Pacific side of divide 5 km W of Sante Fé along road past Escuela Agrícola Alto Piedra, 800-1200 m, 18 March 1973. *Croat 23034* (Holotype: MO!; isotypes: DUKE!, F!, LL!, NY!, USF!). (Fig. 14).

Herbaceous perennials; *rhizomes* repent, 5-18 cm long; internodes 5-8 X 0.5-1.5 mm, moderately pilose with trichomes 0.5-2 cm long, glabrescent with age. *Leaf blades* simple, chartaceous, oblique to transverse, asymmetric, ovate, weakly obovate or suborbicular, 12.5-20.6 X 8.5-15 cm, basally cordate, apically attenuate-acuminate, occasionally abruptly so, marginally ciliate-denticulate, often with a secondary cusp on the side of the blade opposite the petiole insertion, occasionally additional cusps present, glabrous above in intercostal regions but principal nerves moderately to densely hirsute, sparingly hirsute to glandular-hirsute below with trichomes most dense on major nerves, 9-11-palmatinerved. *Petioles* 12.5-31.7 cm X 1.5-4 mm, densely tomentose-pilose when immature but only sparingly to moderately so at maturity with fine sericeous villi 1-2.5 mm long often intermixed with minute glandular trichomes. *Stipules* persistent to subpersistent but often absent from leafless older rhizome segments, reflexed with age, asymmetrically triangular to ovate-triangular, 0.9-1.3 X 0.8-1.1 cm, strongly keeled, apically obtuse to acute, marginally entire, moderately to densely puberulous throughout or glabrous. *Inflorescences* greatly ex-

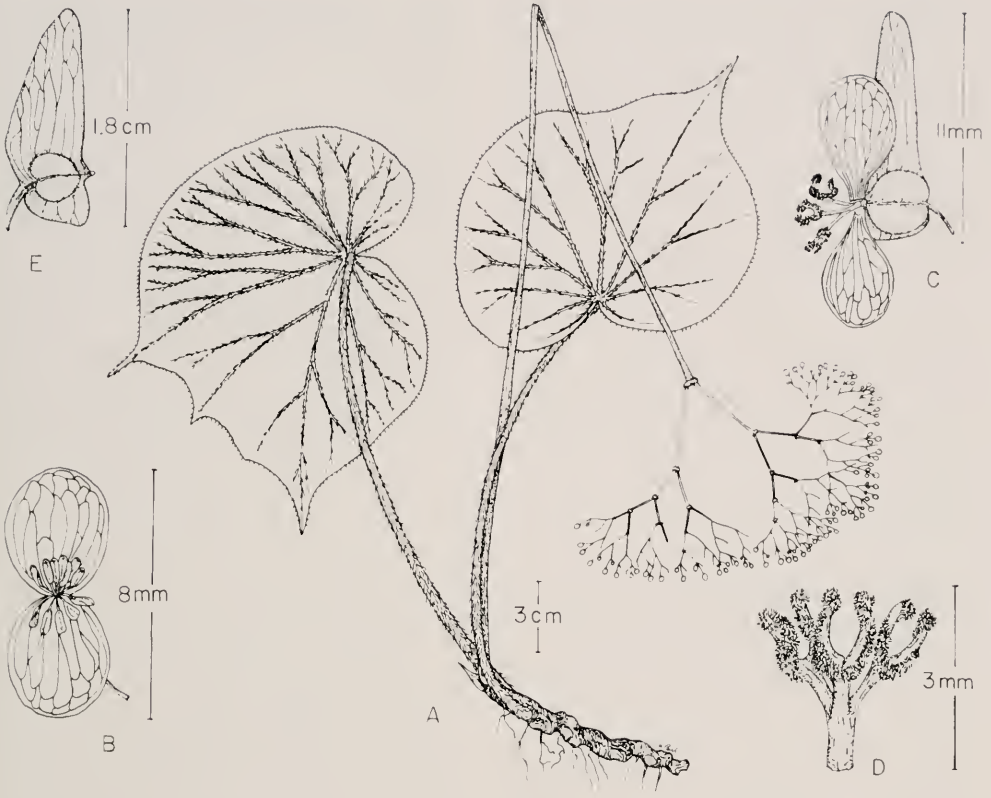

Fig. 14. *Begonia croatii*. A. Habit. B. Staminate flower. C. Pistillate flower. D. Styles and stigmas. E. Capsule. (A, B from *Allen 4375*; C-E from *Croat 23034*).

ceeding the leaves, symmetric to weakly asymmetric, laxly to densely cymose, many-flowered, (7) 9.5-18 cm diam. *Peduncles* 30-68 (108) X 0.3-1 cm, sparingly pilose to tomentose-pilose but glabrate with age. *Bracts* fugacious, not seen. *Staminate flowers*: sepals suborbicular to very broadly transversely elliptic or infrequently ovate, 3-4 X 3.5-4.5 mm, externally glabrous; petals wanting; stamens 11-22; filaments 0.3-1 mm long, borne on a raised torus; anthers oblong to oblong-obovate, 0.8-1.4 X 0.4-0.7 mm. *Pistillate flowers*: pedicels 4.5-8 mm long; bracteoles wanting; sepals narrowly obovate, (3.5) 4.5-7 X 3-4 mm, externally glabrous; petals wanting; ovary 2.5-3 mm long, glabrous; styles 3, 1.5-2 mm long, fused 1/3-1/2 their length; stigmas bicornute. *Capsules* with pedicels (5) 7-16 mm long, trilocular, 4.5-6.5 mm long; locule chambers externally appearing broadly ovate to oblong, 4-5.5 X 4-4.5 mm; wings 3, unequal, the largest slightly asymmetric, narrowly ovate to infrequently oblong, (9) 13-16 X (5) 7-10 mm, apically obtuse, rarely truncate, the second broadly but shallowly asymmetrically triangular, (3.5) 4-6 X (3) 4.5-5 mm, the third subequal to the second, broadly but shallowly lunate, oblong or marginiform.

DISTRIBUTION AND HABITAT: Endemic to western Panama where it is only known from the Santa Fé region between 700-1200 m elevation. (Fig. 11).

FLOWERING: Flowering plants have been collected from February to May.

DISCUSSION: *Begonia croatii* is one of a few species in section *Gireoudia* with a tomentose-pilose petiolar indument formed of sericeous villi, not, as in most members of the section, of whiplash trichomes. It is most similar to *B. urophylla* Hook. but is distinguished from this taxon by its indument, apetalous flowers, smaller sepals (3-4 X 3.5-4.5 vs. 8-15 X 6.5-14.5 mm), fewer (11-22 vs. [23] 33-61) stamens and smaller (4.5-6.5 vs. 6-10 mm) capsules. Although *B. urophylla* is widely distributed in western Panama, it is not known to occur in the Santa Fé region with *B. croatii*. Two radiate inflorescence nodes, persistent to subpersistent stipules and bicornute stigmas readily separate *B. croatii* from *B. quaternata* Smith & Schubert. *Begonia croatii*, like *B. quaternata*, is endemic to western Panama, but it grows in different regions and at different elevations, with *B. croatii* occurring between 700 and 1200 m and *B. quaternata* between 1660 and 2000 m.

SPECIMENS EXAMINED: PANAMA. Veraguas: forested slopes of Cerro Tute in vicinity of Santa Fé, 2500 ft, *Allen 4375* (in part) (MO, No. 1595460, US), primary forest on Caribbean slope above Río Primero Brazo, 5 mi NW of Santa Fé, 700-1200 m, *Croat 23186* (MO); primary forest 0.6 mi beyond Escuela Agrícola Alto Piedra, 730 m, *Croat & Folsom 34026* (MO); steep forested slopes above rock ravine on side of Cerro Tute, above Santa Fé, Pacific slope, *Croat 34225* (MO); 6.4 km outside Santa Fé on road by agriculture school toward cordillera, *Folsom 2946* (MO); NW of Santa Fé, 2.6 km from Escuela Agrícola Alto Piedra, *Mori & Kallunki 4758* (DUKE, MO).

10. *Begonia quaternata* Smith & Schubert, Journ. Wash. Acad. Sci. 40: 244. 1950. TYPE: PANAMA: Chiriquí: vicinity of "New Switzerland", central valley of Río Chiriquí Viejo, 1800-2000 m, January 6-14, 1939, *Allen 1336* (Holotype: US!; isotypes: F!, GH!, MO!, NY!).

Terrestrial herbs; *rhizomes* repent and somewhat succulent, generally unbranched, 5-33 cm long; internodes very short to elongate, 0.3-2 X 0.6-1.8 cm, covered with a dense indument of narrow fimbriate-lacerate scales 3-5 mm long, villi and minute glandular trichomes when immature, but only moderately to sparsely so with age. *Leaf blades* simple, chartaceous to membranaceous, oblique, asymmetric, obovate to suborbicular, 15.5-32 X 11.7-26 cm, basally broadly and deeply cordate with lobes occasionally overlapping, apically abruptly acuminate, marginally irregularly denticulate to dentate at ends of major nerves, above glabrous in intercostal regions but sparingly pilose on principal nerves, beneath intercostal regions glabrous but principal nerves sparsely to moderately pilose with villi and narrow lacerate scales intermixed, the indument 2-5 mm long, 10-14-palmatinerved. *Petioles* 14-32 (45) cm X 2.5-5 (15) mm, moderately to densely squamose or villous-squamose with spreading to retrorse narrow lacerate scales 1.5-6 mm long and occasional villi intermixed with minute glandular trichomes. *Stipules* fugacious to caducous, thick and succulent but scarious when dry, navicular to cucullate, asymmetrically broadly oblong to ovate or when dry appearing suborbicular to transversely ovate, 0.9-1.3 (1.7) X 0.9-1.5 cm, strongly asymmetrically keeled from midlamina to apex, apically rounded to retuse but when dry, frequently splitting and appearing obcordate, marginally entire, glabrous or with a sparse indument of narrow lacerate scales and villi. *Inflorescences* typically exceeding the foliage, cymes symmetric and (2) 3-5 (6) radiate at each lower node but only 2-branched at the upper 2-3 nodes, many-flowered, (6.5) 8-25.5 cm diam. *Peduncles* (20.3) 26.5-58.5 (66) X 0.3-1.4 cm, glabrous or glandular. *Bracts* fugacious, not seen. *Staminate flowers*: pedicels 3.5-12 mm long; sepals white to pale pink but frequently drying light

yellow, broadly ovate to transversely elliptic or suborbicular, 2.5-7 X 2.5-7 mm; petals wanting; stamens (11) 16-27 (30); filaments (0.3) 0.7-1.2 (1.6) mm long, inserted on a raised torus, with a strong tendency toward monadelphy; anthers oblong-elliptic to obovate, 0.5-1 (1.3) X (0.3) 0.4-0.7 (0.8) mm. *Pistillate flowers*: pedicels 2.5-7 (13) mm long; bracteoles wanting; sepals colored like staminate sepals, broadly elliptic or transversely broadly elliptic to suborbicular, 3-6.5 X 3-6 mm; petals wanting; ovary 3-5.5 (7) mm long; styles 3, 1.3-2 mm long, connate 1/3-1/2 their length; stigmas broadly lunate. *Capsules* with pedicels (4.5) 6-11 (16) mm long, trilocular, 5-7.5 (12) mm long; locule chambers externally appearing broadly ovate to oblong-elliptic, 4-6 (8) X 3-6 mm; wings 3, unequal, the largest asymmetrically triangular, 4-7 (10) X 3.5-6.5 (9) mm, apically subacute to obtuse, the second asymmetric, broadly triangular, 3-5.5 X 3.5-6 (10.5) mm, apically generally obtuse, the third marginiform or broadly but shallowly triangular.

DISTRIBUTION AND HABITAT: *Begonia quaternata* is known only from Chiriquí Province in western Panama and adjacent Costa Rica where it occurs at elevations between 1600-2010 m in both wet montane primary forests and along roadbanks among disturbed secondary vegetation. It is locally abundant on the W slopes of Volcán Chiriquí Viejo between Cerro Punta and Bambito and on steep, rocky hillsides in the Llanos del Volcán. (Fig. 15).

FLOWERING: Flowering specimens have been gathered from November through February.

DISCUSSION: *Begonia quaternata* is unique among Mesoamerican begonias in bearing inflorescences whose lower nodes are typically three to five radiate, but only infrequently two radiate. Regardless of the number of branches at lower nodes, upper nodes resemble those of other species in sect. *Gireoudia* and are characteristically two-branched. This unusual inflorescence character together with the fugacious to early caducous, squamose, cucullate stipules, large broad obovate to suborbicular leaf blades, squamose petioles, small monadelphous to submonadelphous stamens and small capsules readily distinguish *B. quaternata*

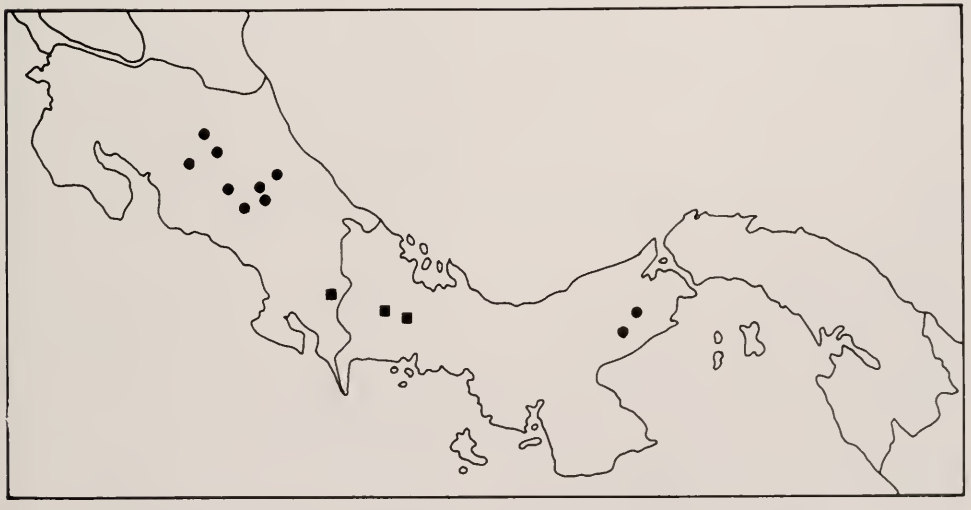

Fig. 15. Distribution of *Begonia conchifolia* (circles) and *B. quaternata* (squares).

from other Central American species in sect. *Gireoudia*.

Together *B. quaternata*, *B. urophylla* and *B. croatii* constitute the urophylla species group. Among this group *B. quaternata* is unusual with its 2-6 radiate lower inflorescence nodes, caducous stipules which often appear obcordate when dry and submonadelphous to monadelphous filaments. *Begonia quarternata* also may be separated from *B. urophylla* which occurs in Chiriquí Province, Panama, by its smaller sepals, fewer stamens, broadly lunate stigmas and smaller capsules (Table 5). The relationship of *B. quaternata* to *B. croatii* is pursued under that taxon.

SPECIMENS EXAMINED: COSTA RICA: Puntarenas: upper Río Burú, 2010 m, *Gómez et al. 21418* (MO). PANAMA: Chiriquí: Cerro Horqueta, E facing slope above Quebrada Horqueta, opposite Cerro Horqueta, 1660-1700 m, *Cochrane, Cochrane & Kowal 6234* (F, MO, WIS); Bambito, *Croat 10618* (MO); 2 mi N of El Hato del Volcán, *Croat 10662* (MO); vicinity of Methodist Camp near Nueva Suiza, *Croat 13512* (MO, NY); forested hill north of Audubon Cabin, *Croat 13621* (NY, MO); about 9 mi by road WNW of Boquete, 1870 m, *Davidse & D'Arcy 10298* (MO); NW of Boquete, Cerro Horqueta, 5000-5800 ft, *Dwyer et al. 459* (GH, MO); mixed evergreen forest 5.5 mi S of Cerro Punta along cleared path, 1700 m, *Graham 277* (GH, MICH, MO); grassy slopes on lava flow about 16 km above town at Volcán, 5900 ft, *Hammel 1566* (MO); llano E of El Hato del Volcán, *Hammel et al. 6795* (MO); 1.5 mi W of Cerro Punta, humid oak-laurel forest near Río Chiriquí Viejo, 1700 m, *McDaniel 10107* (MO); Bambito, across road from Río Chiriquí Viejo, 5255 ft, *Utley 5688* (B, C, DUKE, GH, K, MICH, MO, NY, US); Llanos del Volcán, 3.1 km from El Hato del Volcán, 5900 ft, *Utley 5689* (CAS, DUKE, MEXU, MO, NY, WIS, US); between Cerro Punta and Bambito, *Wilbur et al. 10958* (DUKE).

11. *Begonia strigillosa* A. Dietr., Allg. Gartenzeit. 19: 330. 1851. TYPE: CENTRAL AMERICA: Chiriquí:

TABLE 5. Morphological comparison of *Begonia croatii*, *B. quaternata* and *B. urophylla*.

	B. croatii	*B. quaternata*	*B. urophylla*
Upper leaf surface	principal nerves moderately-densely hirsute	sparsely pilose on principal nerves	hirsute, only rarely glabrous
Leaf blade size (cm)	12.5-20.6 X 8.5-15	15-32 X 11.7-26	(8.1)10.4-29.3 X (4.3)6-16(19.7)
Petiole length (cm)	12.5-31.7	14-32(45)	(6.5)11-30.5(52)
Petiolar indument	tomentose-pilose	squamose	squamose to villous-squamose
Trichome type	fine, sericeous villi	narrow entire to broad lacerate scales	narrow entire to broad lacerate scales
Stipules	persistent to subpersistent	fugacious-caducous	subpersistent
Branches per inflorescence node	2	(2)3-5(6)	2
Staminate sepals	3-4 X 3.5-4.5	2.5-7 X 2.5-7	(8)11-15 X (6.5)10-14.5
Stamen number	11-22	(11)16-27(30)	(23)33-61
Filaments	free	submonadelphous to monadelphous	free
Stigma shape	bicornute	lunate	bicornute
Capsule length (mm)	4.5-6.5	5-7.5(12)	(6)7-10

without further locality, described from material cultivated from seeds sent by Warscewicz to Berlin; (Holotype not seen and perhaps non-existent).

Gireoudia strigillosa (A. Dietr.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

Begonia daedalea Lem., Ill. Hortic. 7: misc. 54. 1860; Ill. Hortic. 8: pl. 269. 1861. TYPE: MEXICO: exact locality unknown, described from cultivated material taken to Paris by Ghiesbreght (Holotype: not seen and perhaps non-existent).

Begonia barbana C.DC., Bull. Soc. Bot. Belg. 35. pt. 1: 261. 1896. TYPE: COSTA RICA: Heredia: forêt de la Esmeralda massif du Barba, 2000 m, *Biolley 7257* (Lectotype; G!, isolectotypes: BR!, US!).

Begonia tinctoria Smith & Schubert, Contr. Gray Herb. 127: 29. 1939. TYPE: GUATEMALA: Suchitepéquez: Finca Moca, 4800 ft, *Skutch 1556* (Holotype: GH!).

Acaulescent or rarely caulescent herbs; *rhizomes* repent, usually branching with age, short to elongate, 2-11 (39) cm long; internodes generally short, rarely elongate, 0.2-0.8 (3.2) cm X (3) 4-14 mm, lenticellate, sparsely to moderately squamose throughout, with trichomes 2-6 mm long; nodes with scales forming a conspicuous band around the petiole base. *Leaf blades* simple, membranaceous to subcoriaceous, oblique to transverse, asymmetric, vary narrowly to broadly ovate, oblong or subelliptic, (3.8) 7-14 (18.5) X (2) 4.1-9.3 cm, basally usually broadly, shallowly cordate but occasionally deeply, narrowly cordate, lobes generally not overlapping, apically attenuate-acuminate, marginally ciliate, ciliate-denticulate and usually broadly dentate at ends of major nerves, infrequently doubly dentate or doubly serrate, occasionally with a broad shallow, obtuse to acuminate lobe opposite the petiole insertion, dark green or occasionally sparingly to densely maculate and glabrous above but beneath light green with frequently deep red primary nerves and glabrous to glandular-puberulous intercostal regions and sparingly squamose, villous-squamose or villous primary nerves, 7-10 (11)-palmatinerved. *Petioles* light green, frequently maculate, (3) 6.3-18 (29.5) cm X 1-3 (7) mm, indument variable, densely squamose to villous-squamose or villous, consisting of narrow to broad, entire to lacerate scales, coarse villi or a mixture of scales and coarse villi often with minute glandular trichomes intermixed, trichomes translucent white becoming deep red basally, 3-6 mm long. *Stipules* persistent, translucent light green, becoming spreading to reflexed with age, asymmetric, narrowly ovate or triangular to broadly lanceolate (5) 7-15 mm X 4-8.3 mm, strongly keeled, apically obtuse to acuminate, marginally entire, usually glabrous or rarely puberulous but the keel often fimbriate-laciniate. *Inflorescences* generally exceeding the foliage, symmetric to moderately asymmetric, laxly cymose, usually few-flowered, but occasionally many-flowered, (1.5) 2.5-12 (15) cm diam. *Peduncles* light green, often suffused with dark red, frequently maculate, (5) 6.8-22.9 (31.5) cm X 1-3 (5) mm, glabrous to sparingly villous or villous-squamose and often sparingly glandular. *Bracts* caducous, light green, the lowermost navicular, narrowly elliptic to ovate, 1.1-1.5 X 0.7-0.9 cm, unkeeled to weakly keeled distally, apically acuminate, marginally entire, glabrous to sparingly glandular throughout.

Staminate flowers: pedicels 6-18 (24) mm long; sepals white to pale or dark pink, elliptic to broadly elliptic, suborbicular, subrhomboid or transversely elliptic, 6-10 mm X 5.5-10 mm, glabrous to sparingly glandular; petals wanting; stamens 6-17; filaments 0.5-1.5 mm long, borne on a low to slightly raised receptacle; anthers oblong-obovate or subelliptic, 1.3-2 X (0.5) 0.8-1 mm. *Pistillate flowers*: pedicels 4-14 mm long; bracteoles wanting; sepals colored like the staminate sepals, transversely elliptic, suborbicular to obovate, 5-9 X 5-7 mm, glabrous to glandular; petals wanting; ovaries (5) 7.5-11 mm long, glabrous or sparingly glandular throughout; styles 3, 1-2 mm long, connate 1/4-1/2 their length; stigmas lunate. *Capsules* with pedicals 8-21 (30) mm long, trilocular, 9-16 mm long; locule chambers externally appearing narrowly to broadly oblong or ovate, 5.5-8 (11) X 3-6.5 (8.5) mm; wings 3, subequal or rarely unequal, variable in form, the largest broadly but shallowly asymmetrically triangular or lunate-triangular, (5) 5.5-12 (14) X (7) 10-15 mm, apically obtuse to truncate or acute to subacute, rarely acuminate, the second usually similar to the first, 5-9 X 9-14 mm, the third shallowly lunate or lunate-triangular, 4-6 (9) X 7-11 mm.

DISTRIBUTION AND HABITAT: *Begonia strigillosa* ranges from Chiapas in southern Mexico to western Panama where it occurs at elevations between 1350-2800 m. In Costa Rica *B. strigillosa* is most abundant on the drier Pacific slopes of the cordilleras where it frequently forms large populations on forested lower montane and montane slopes. It often colonizes mossy rocks and lower portions of tree trunks that are devoid of other flowering plants (Fig. 13).

FLOWERING: *Begonia strigillosa* flowers most profusely during the latter part of the rainy season from August to December and only sporadically during other months.

DISCUSSION: The specimen commonly accepted as the type of *B. strigillosa* is from Hort. Bot. Berol. and was prepared in 1856, 5 years after Dietrich described this species. With the exception of the identification, all relevant label information appears to have been inscribed by Klotzsch when he was working on his treatment of the Begoniaceae. This specimen, therefore, cannot be considered the type of *B. strigillosa*. A second undated sheet consisting of a single leaf is also based on Warscewicz material from Central America but came from Hort. Bergemann. Although this specimen was determined as *B. strigillosa* by Dietrich, it also should not be considered a type of *B. strigillosa* because Dietrich in his protologue clearly indicated that Warscewicz sent seed to them at Berlin.

Although no authentic specimen of *B. daedalea* Lem. was available for study, both Lemaire's description and illustration are well within the variability presently recognized in *B. strigillosa*. Alphonse de Candolle (1864) and Smith and Schubert (1958, 1961) also considered *B. daedalea* to be conspecific with *B. strigillosa*. Citing Lemaire's description in which he characterized the leaves as being peltate and his illustration depicting highly maculate leaves, Ziesenhenne (1970) contends that *B. daedalea* is distinct from *B. strigillosa*. Lemaire may have chosen an unfortunate word to describe leaf shape, because the blades are unequivocally cordate and palminerved in his illustration. Leaf maculation is highly variable in *B. strigillosa*, with populations from lower Central America being emaculate while those from Guatemala and Mexico often contain individuals with maculate leaves. Illustrating the potential problem with utilizing leaf maculation as an important

taxonomic character is a specimen of *B. strigillosa* at the U.S. National Herbarium, *Williams 26198* from Guatemala, which contains individuals with maculate leaves and a plant with emaculate leaves. Both *B. tinctoria* and *B. barbana* are also considered to be conspecific with *B. strigillosa*. When Smith and Schubert described *B. tinctoria* in 1939, little material of *B. strigillosa* was available for study, and *Skutch 1556*, with its villous indument and subequal capsule wings, appeared distinctive. *Begonia barbana* previously has been treated in synonymy with *B. strigillosa* by Smith and Schubert (1958, 1961). I have selected a lectotype for this taxon, *Biolley 7257* at Geneva. One of the other specimens cited by Casmir de Candolle, *Pittier 3908* from near Buenos Aires, Costa Rica, is referrable to *B. plebeja*.

Begonia strigillosa exhibits variation in several vegetative and capsular characters. While rhizomes on most specimens are acaulescent, specimens from several localities near San Martín Chile Verde in the department of Quetzaltenango, Guatemala, including *Standley 83720* and *Standley 85183*, have caulescent rhizomes with elongate internodes that may potentially function as runners. This perplexing growth form has not been observed within populations of *B. strigillosa* from southern Central America, and more collections are necessary before the significance of this character can be interpreted. The petiole indument ranges from broad, lacerate scales to coarse villi in specimens studied, and individuals frequently contain a mixture of both trichome forms. Although the extremes were never encountered in the same population, both forms are found throughout the entire range of this species and do not appear to be correlated with any other variable character. Similar variability in petiole vestiture has been observed in *B. heracleifolia*.

Most capsular characters are variable in size and form. On specimens gathered in Costa Rica and Panama, locule chambers appear oblong or only slightly ovate, but on material from Guatemala and Mexico they often appear broadly ovate. Along with these differences, the shape of the wings and size relative to one another often differ. While the wings usually are considered to be subequal, when numerous collections were examined it was obvious that there was a continuum from capsules with strongly subequal or unequal wings to capsules with only slightly subequal wings. There seems to be significant interpopulational variation in wing characters with populations from adjacent areas like *Utley 5772* and *Utley 5777* from the Altos de Tablazo in Costa Rica being most similar but very different from *Utley & Utley 4566* which was collected on the southern slopes of Volcán Barba in Costa Rica.

Begonia strigillosa appears to be most closely related to *B. morii* and *B. louis-williamsii*. Relationships within the strigillosa species group are pursued in discussions of *B. morii* and *B. louis-williamsii* and are summarized in Table 6.

SPECIMENS EXAMINED: MEXICO. Chiapas: barrio of Chihk Ha′, paraje of Yashanal, Municipio of Tenejapa, 5500 ft, *Breedlove 9409* (DS, US); montane rain forest 45-50 km NE of Huixtla along rd to Motozintla, Municipio of Motozintla de Mendoza, 1900 m, *Breedlove & Smith 22609* (DS); *Breedlove & Thorne 30977* (DS); SW slope of Volcán Tacaná above Talquián, Municipio of Unión Juárez, *Breedlove 42508* (DS); rd from Toliman to Niquivil near Ojo de Agua, Municipio of Motozintla de Mendoza, 2000 m, *Breedlove 42662* (DS); cliffs, S exposure, Volcán Tacaná, 6000 ft, *MacDougall s.n.* (NY). GUATEMALA. Chimaltenango: Barranco de La Sierra, SE of Patzúm, 2100 m, *Standley 61522* (F, NY). Guatemala: Pacaya, 7000 ft, *Kellerman s.n.* (US); above Las Calderas, Volcán de Pacaya, 1800-2000 m, *Standley 58416* (F). Huehuetenango: Río Azul below Jacaltenango, Sierra de los Cuchumatanes, 1400 m,

TABLE 6. Morpholopical comparison of *Begonia louis-williamsii*, *B. morii* and *B. strigillosa*.

	B. louis-williamsii	*B. morii*	*B. strigillosa*
Upper leaf surface	hirsute	glabrous	glabrous
Leaf blade size (cm)	8.7-13 X 3.7-5.7	(5.7)9-16 X (3.8)5.3-11.1	(3.8)7-14(18.5) X (2)4.1-9.3
Petiolar indument	squamose with lacerate scales	villous	squamose, villous-squamose or villous
Staminate sepals (mm)	14-17 X 12-17	(5)7-11 X 6-8.5	6-10 X 5.5-10
Stamens	16-18	15-28	6-17
Stigma shape	bicornute	lunate	lunate
Ovary length (mm)	7-9	5-6	(5)7.5-11
Capsule wings	unequal	unequal	subequal, rarely unequal

Steyermark 51853 (F, GH). Quetzaltenango: Finca Pirineos, below Santa María de Jesús, 1350-1380 m, *Standley 68249* (F); Las Nubes, S of San Martín Chile Verde, 2250 m, *Standley 83706* (F, GH); *Standley 85183* (F, GH); Boxantín, SE of San Martín Chile Verde, 2400 m, *Standley 83712* (F); *Standley 83720* (F); *Standley 83727* (F); Río Samala near Santa María de Jesús, 1500-1560 m, *Standley 84675* (F); lower slopes of Volcán de Zunil on rd to Fuentes Georginas, 2200-2350 m, *Standley 85820* (F, GH); old rd between Finca Pirineos and Patzulin, 1200-1400 m, *Standley 86891* (F); Quebrada San Geronimo, Finca Pirineos, lower S facing slopes of Volcán Santa María between Santa María de Jesús and Calahuaché, 1300-2000 m, *Steyermark 33346* (F); Volcán Zunil, 2500-3800 m, *Steyermark 34627* (F, US). San Marcos: above Río Tacaná near San Antonio, 2700 m, *Standley 66173* (F); NW slopes of Volcán Tajumulco, 2300-2500 m, *Steyermark 36577* (F); 1800-2500 m, *Steyermark 36819* (F); 2300-2800 m, *Steyermark 36895* (F, US); above Finca El Porvenir, along Río Cabús, S facing slopes of Volcán Tajumulco, 1300-1500 m, *Steyermark 37996* (F); rugged canyon S of San Marcos toward Castalia, 1600-2200 m, *Williams, Molina & Williams 26198* (F, NY, US). EL SALVADOR. San Salvador: W slopes above Finca Florencia, 1680-1890 m, *Carlson 392* (F). COSTA RICA. Alajuela: Zarcero, *Smith A584* (F); Pacific cloud forest, San Luis de Zarcero, 1525 m, *Smith P2055* (GH, US); dry woodland, Zarcero, 1900 m, *Smith RZ32* (US); S slope of Volcán Poás, La Ventolera, 1700 m, *Standley 34680* (US). Heredia: Volcán Barba, 2000 m, *Leon 88* (CR); *Tonduz 1333* (BR, CR, G, US); CR114, 1.7 km W of Porrosatí along rd to Sacramento, 1900-2000 *Utley & Utley 4566* (DUKE). Puntarenas: primary forest along Río Coto Brus near Coton, *Croat 26612* (MO). Puntarenas-Alajuela border: Monteverde Nature Reserve, 1450-1650 m, *Burger & Baker 9674* (F). San José: near Río Parrita Chiquita 5 km N of Santa María de Dota, 2000 m, *Lent 3936* (US); moist forest between Aserrí and Tarbaca, 1600-1900 m, *Standley 34152* (US); vicinity of Santa María de Dota, 1500-1800 m, *Standley 41820* (US); *Standley 42477* (US); *Standley & Valerio 43309* (US); near Quebradillas, about 7 km N of Santa María de Dota, 1800 m, *Standley 42998* (US); Cerro Daser in Serros de Escazú, 1900 m, *Utley 5749* (B, CR, DUKE, MO); SE of Higuito on dry road banks along Calle Tablazo, Altos de Tablazo, *Utley 5772* (DUKE, MEXU, US); *Utley 5777* (DUKE, F). Without further locality, *Pittier s.n.* (BR). PANAMA. Chiriquí: 1.5 mi W of Cerro Punta near Río Chiriquí Viejo, 1700 m, *McDaniel 10127* (MO). CENTRAL AMERICA: Without locality (B).

12. *Begonia louis-williamsii* Burt-Utley, Brittonia 34: 194. 1982. TYPE: GUATEMALA :San Marcos: wet mountain forest near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, W facing slope of Sierra Madre Mountains, 1800-2400 m, 10-18 December 1963. *Williams, Molina & Williams 25822* (Holotype: F!; isotypes: NY!, US!) (Fig. 16).

Acaulescent herbs; *rhizomes* repent, 6-9 cm long; internodes (0.2) 0.5-1.6 cm X 2-8 mm, glandular to villous-squamose or squamose, with narrow to broad entire or lacerate scales 1-2 mm long often inter-

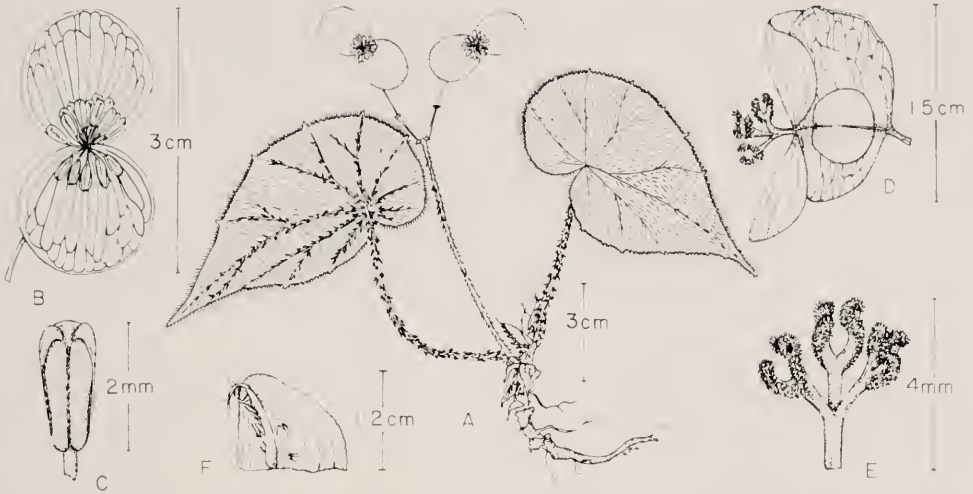

Fig. 16. *Begonia louis-williamsii*. A. Habit. B. Staminate flower. C. Stamen. D. Pistillate flower. E. Styles and stigmas. F. Stipule. (from *Williams, Molina & Williams 25822*)

mixed with coarse whiplash trichomes. *Leaf blades* simple, chartaceous to subcoriaceous, oblique to transverse, narrowly oblong-elliptic, 8.7-13 X 3.7-5.7 cm, basally cordate, apically attenuate-acuminate, marginally long-ciliate, ciliate-denticulate to ciliate-serrulate and dentate to doubly dentate or serrate at ends of major nerves, hirsute with trichomes 1-3 mm long above and beneath, except the principal nerves below which are moderately to densely squamose, 9-10-palmatinerved. *Petioles* 4.7-21.3 cm X 1-2 mm, moderately to densely glandular-squamose with spreading lacerate scales (1) 2-3 mm long intermixed with minute glandular trichomes. *Stipules* persistent, asymmetrically broadly ovate, 0.7-1.4 X 0.6-1.2 cm, strongly keeled, apically obtuse to subacute, marginally entire, lamina glabrous to very sparingly glandular-squamose, but the keel usually fimbriate-lacerate. *Inflorescences* equal to or shorter than the foliage, symmetric, laxly cymose, few-flowered, 2.5-7.5 cm diam. *Peduncles* 6.5-17.5 cm X 0.5-2.5 mm, sparsely squamose to villous-squamose. *Bracts* fugacious, not seen. *Staminate flowers*: pedicels 1.3-2 cm long; sepals suborbicular, broadly transversely elliptic or elliptic-obovate, 1.4-1.7 X 1.2-1.7 cm, glabrous; petals wanting; stamens 16-18; filaments 1-2 mm long, borne on a very low receptacle; anthers narrow, oblong to oblong-obovate, 1.3-2 X 0.6-0.9 mm. *Pistillate flowers*: pedicels 1.6-1.7 cm long; bracteoles wanting; sepals suborbicular, 0.9-1.3 X 0.9-1.2 cm, glabrous; petals wanting; ovary 7-9 mm long, sparingly glandular throughout; styles 3, 2.5-3 mm long, connate 1/3-1/2 their length; stigmas bicornute. *Capsules* not seen.

DISTRIBUTION AND HABITAT: Only known from wet mountain forests and cloud forests in the Sierra Madre Mountains in the department of San Marcos, Guatemala where it occurs between 1800-2400 m elevation (Fig. 13).

FLOWERING: Flowering specimens have been collected in December and January.

DISCUSSION: *Begonia louis-williamsii* is characterized by narrowly oblong-elliptic leaves with long attenuate-acuminate apices, hirsute adaxial leaf surfaces,

squamose petioles, few-flowered symmetric, cymose inflorescences, large staminate and pistillate sepals and bicornute stigmas. Although capsules are lacking, certain aspects of wing morphology can be inferred from ovaries of pistillate flowers at anthesis. The wings are unequal, the largest appearing broadly oblong to subelliptic, the other two well-developed and asymmetrically triangular.

Begonia louis-williamsii belongs to the strigillosa species group along with *B. strigillosa* and *B. morii*. These taxa are characterized by similar blade sizes and shapes, squamose, villous-squamose or villous induments, similar ranges in stamen number and well-developed capsule wings. *Begonia louis-williamsii* has been confused with *B. strigillosa* because of similar leaf size and usually few-flowered inflorescences, but differs in several significant characters. The upper leaf surfaces of *B. louis-williamsii* are conspicuously hirsute, while those of *B. strigillosa* are glabrous. Frequently the petiolar indument is villous-squamose or villous in *B. strigillosa* whereas only squamose induments have thus far been observed in *B. louis-williamsii*. When pistillate flowers or capsules are available, the bicornute stigmas and unequal ovary or capsule wings of *B. louis-williamsii* will distinguish it from *B. strigillosa,* which has lunate stigmas and characteristically subequal capsule wings. Although *B. strigillosa* frequently has large staminate sepals, they are smaller than those observed on *B. louis-williamsii*. With the exception of wing form, these same characters also separate *B. louis-williamsii* from *B. morii*. The differences among members of this species group are summarized in Table 6. The only other rhizomatous species occuring in Guatemala with an indument and stigma form similar to *B. louis-williamsii* is *B. urophylla*. *Begonia louis-williamsii* is easily separated from this taxon by its generally smaller size, somewhat narrower leaf blades, larger sepals and fewer stamens.

SPECIMENS EXAMINED: GUATEMALA. San Marcos: montane cloud forest area on outer slopes of Tajumulco Volcano, Sierra Madre Mountains about 8-10 km W of San Marcos, 2300 m, *Williams et al. 26810* (F).

13. *Begonia morii* Burt-Utley, Brittonia 34: 192. 1982. TYPE: PANAMA: Panamá: 5-10 km NE of Altos de Pacora about 15 km from Cerro Azul, 5 January 1975, *Mori, Kallunki & Gentry 4204* (Holotype: MO!; isotypes: DUKE!, US!). (Fig. 17).

Acaulescent herbs; *rhizomes* repent, branched or simple, 2.5-7.9 cm long; internodes 0.2-0.4 (1) X 0.4-1.1 cm, sparingly to moderately villous throughout, nodes frequently with a sparse band of narrow lacerate scales surrounding the petiole base or leaf scar. *Leaf blades* simple, chartaceous, oblique to transverse, narrowly to broadly ovate, oblong, suborbicular or infrequently obovate, (5.7) 9-16 X (3.8) 5.3-11.1 cm, basally cordate, apically acuminate to attenuate-acuminate, marginally ciliate, obsoletely undulate, infrequently denticulate or irregularly dentate, and occassionally with a broad but shallow rounded lobe on the side of the blade opposite the petiole, glabrous above and glandular-hirsute beneath with trichomes most dense on principal nerves, palmately 9-10-nerved. *Petioles* (4.5) 7-14.7 cm X 1-2.5 mm, moderately to densely villous or glandular-villous with trichomes (2) 3-4 mm long often intermixed with narrow entire scales. *Stipules* persistent, asymmetrically narrowly triangular, (5) 8-12 X (4) 6-8 mm, strongly keeled. *Inflorescences* often greatly exceeding the

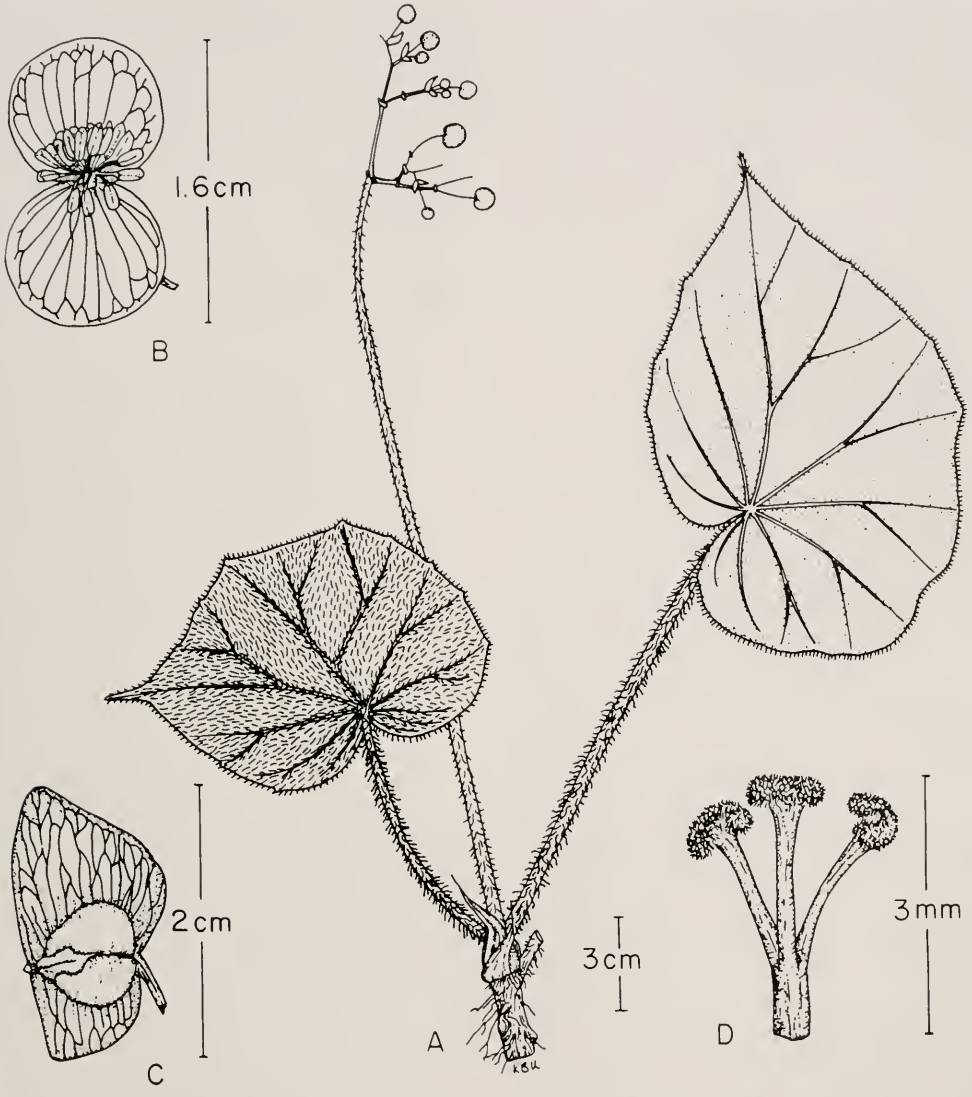

Fig. 17. *Begonia morii*. A. Habit. B. Staminate flower. C. Capsule. D. Styles and stigmas. (from *Mori, Kallunki & Gentry 4204*).

foliage, strongly asymmetric, laxly cymose when mature, few- to many-flowered, 3-10 cm diam. *Peduncles* (10) 16-45.5 cm X 1-4 mm, sparingly glandular-pilose. *Bracts* caducous, the lowermost occasionally navicular, obovate-elliptic or broadly ovate, 8 X 4-6 mm. *Staminate flowers*: pedicels 6-13 mm long; sepals broadly ovate, suborbicular or transversely elliptic, (5) 7-11 X 6-8.5 mm, externally glandular; petals wanting; stamens 15-28; filaments 0.3-1.6 mm long, borne on a raised torus and often appearing submonadelphous; anthers oblong to obovate, 1-1.5 X 0.4-0.6 mm. *Pistillate flowers*: bracteoles wanting; sepals transversely elliptic or reniform, mature sepals not seen and their size therefore unknown; petals wanting; ovary 5-6 mm long, glandular through-

out; styles 3, 3 mm long, connate to 1/3 their length; stigmas lunate. *Capsules* with pedicels 12-18 mm, trilocular, 9 mm long; locules externally appearing ovate, 8.5-9 X 7.5 mm; wings 3, unequal, the largest asymmetric, ovate, 12-13 X 11-13 mm, the second broadly but shallowly asymmetrically triangular, 6.5 X 9 mm, the third broadly lunate, 6.5 X 9 mm.

DISTRIBUTION AND HABITAT: Endemic to Panama where it occurs in parts of Panama Province E of the Canal Zone (Fig. 11).

FLOWERING: Flowering material has been gathered during December and January.

DISCUSSION: Persistent reflexed stipules, densely villous petioles, glabrous upper leaf surfaces, unilateral inflorescences, 15 to 28 stamens borne on a raised torus, ebracteolate pistillate flowers, lunate stigmas and unequal capsule wings characterize *B. morii*.

Begonia morii superficially resembles those populations of *Begonia strigillosa* A. Dietr. with villous petiolar induments in its ovate, oblong or rarely suborbicular leaves, glabrous upper leaf surfaces, blade, petiole and sepal dimensions and in its lunate stigmas. It differs from *B. strigillosa* in its frequently longer peduncles, more numerous stamens and unequal capsule wings. While only a few specimens of *B. morii* are presently available, none have the conspicuous squamose or villous-squamose indument that is so frequently observed on specimens of *B. strigillosa*. Inflorescences of *B. morii* are strongly asymmetric to unilateral while those of *B. strigillosa* are only weakly to moderately so. These species also have different elevational and geographic distributions in Panama. *Begonia morii* is known only from eastern Panama at elevations under 350 m, whereas *B. strigillosa* has not been found in Panama east of the Chiriquí region where it occurs at elevations around 1700 m (Table 6). *Begonia morii* is distinguished from *B. buseyi* by its oblique to transverse basally cordate leaves, blade size and shape, more numerous stamens, and larger capsules with broadly ovate primary wings.

SPECIMENS EXAMINED. PANAMA. Panamá: tributary of Río Chagres 5 mi SW of Cerro Brewster, sandy and rocky river beds, 1000 ft, *Lewis et al. 3380* (DUKE, MO).

14. *Begonia nelumbiifolia* Schlecht. & Cham., Linnaea 5: 604. 1830. TYPE: MEXICO: in sylvis umbrosis Misantlae, February 1829, *Schiede 730* (Lectotype: B!; isolectotypes: B! [2 sheets], HAL!).
Gireoudia nelumbiifolia (Schlecht. & Cham.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.
Begonia deryckxiana Lem., Hort. Univ. Misc. 5: 355. 1844. TYPE: Locality unknown, described from material cultivated at Brussels (Holotype not seen and perhaps nonexistent).
Begonia caudilimba C.DC., Smithson. Misc. Coll. 69(12): 9. 1919. TYPE: Canal Zone: Forest along the Río Indio de Gatún, near sea level, *Maxon 4866* (Holotype: US!; isotype: NY!).

Herbaceous perennials; *rhizomes* repent, 0.04-1.6 m long; internodes short, 0.4-2 X 0.7-2.8 cm, densely villous with an indument of villi intermixed with narrow barbate, basally rounded or flattened trichomes 2-6 mm long. *Leaf blades* simple, chartaceous to subcoriaceous, oblique, obovate, broadly ovate, elliptic or rarely suborbicular, 15-40 X 11-32 cm, basally peltate, apically acuminate, attenuate-acuminate or infrequently acute, marginally ciliate-denticulate and often dentate, glabrous throughout above

or the principal nerves only sparingly hirsute, and beneath glabrous, glandular or rarely hirsute in intercostal regions but sparsely hirsute to glandular-hirsute on principal nerves, 7-9-peltinerved. *Petioles* 11-63.5 cm X 2-7 (11) mm, sparsely to moderately hirsute when immature with spreading to retrorse whiplash trichomes (0.3) 1-4 mm long intermixed with minute glandular trichomes, but glabrate with age. *Stipules* persistent, asymmetrically triangular to lanceolate, 1.6-3 X 1.1-1.8 cm, strongly keeled with the costa excurrent apically or subapically, marginally entire or weakly denticulate and ciliate, especially apically; hirsute throughout or the keel only hirsute. *Inflorescences* commonly exceeding the foliage, symmetric to weakly asymmetric, regularly laxly to densely cymose, many-flowered, 7-28 cm diam. *Peduncles* (32.4) 40-142 X 0.2-1.2 cm, often appearing glabrous but sparsely glandular or glandular-pilose, becoming glabrate with age. *Bracts* caducous, ovate to obovate, weakly keeled, marginally entire or ciliate-denticulate to ciliate-serrulate, glabrous to sparingly hirtellous. *Staminate flowers*: pedicels 5-8 mm; sepals succulent, white to pale pink, suborbicular to broadly ovate or oblong-elliptic, 4-6 X 4-6.5 mm, glabrous to sparingly glandular externally; petals wanting; stamens 13-38 (46); filaments 0.2-1 mm long, borne on a raised torus; anthers oblong to oblong-obovate, 0.8-1.6 (2) X 0.4-0.8 mm. *Pistillate flowers*: pedicels (3) 6.5-10 (13) mm long; bracteoles wanting; sepals colored like staminate sepals, suborbicular, ovate or obovate, 4-7 X 3.5-7 (8) mm; petals wanting; ovary 4.5-7 (8) mm long, glabrous to sparingly glandular; styles 3, 1.3-2 mm long, connate briefly basally, stigmas very broadly lunate to bicornute, spiralling at the ends. *Capsules* with pedicels 9-20 (27) mm long; trilocular, 6-9.5 (14) mm long; locule chambers externally appearing suborbicular to broadly oblong or ovate, 5-7 (11) X 3.5-5.5 (9) mm; wings 3, unequal, the largest asymmetric, ovate to oblong or occasionally elliptic, (4.5) 7-13 (19) X 7-13 (18) mm, apically obtuse to subacute or truncate, the second narrowly lunate to asymmetrically lunate, 3.5-9 X 7-13 mm, the third equal or subequal to the second or marginiform.

DISTRIBUTION AND HABITAT: Central Mexico to Colombia from near sea level to 1000 m elevation. *Begonia nelumbiifolia* has not been reported from Honduras, Nicaragua, or western Panama. While commonly encountered in Mexico and Guatemala, this species has only recently been collected in Costa Rica (*Gómez 19567*) and is only rarely collected from the Canal Zone or in eastern Panama. Considering the inaccessibility of much of the Caribbean watershed of Central America, the lack of collections is not totally unexpected. (Fig. 18).

FLOWERING: Principally December to May but sporadically at other times.

DISCUSSION: *Begonia nelumbiifolia* is one of the most easily recognized species within sect. *Gireoudia* because of its unusually large, peltate leaves and many-flowered symmetric inflorescences with ebracteolate pistillate flowers. Since individuals are frequently very large, prepared specimens of *B. nelumbiifolia* often lack rhizomes, petioles and complete peduncles. The observed variation in leaf blade size may actually underestimate that which occurs in individual plants or in populations, as leaf blades of a convenient size or sufficiently small plants may be selected for pressing by botanists with no particular interest in *Begonia*. Although pistillate flowers of *B. nelumbiifolia* are characteristically ebracteolate, close examination of speci-

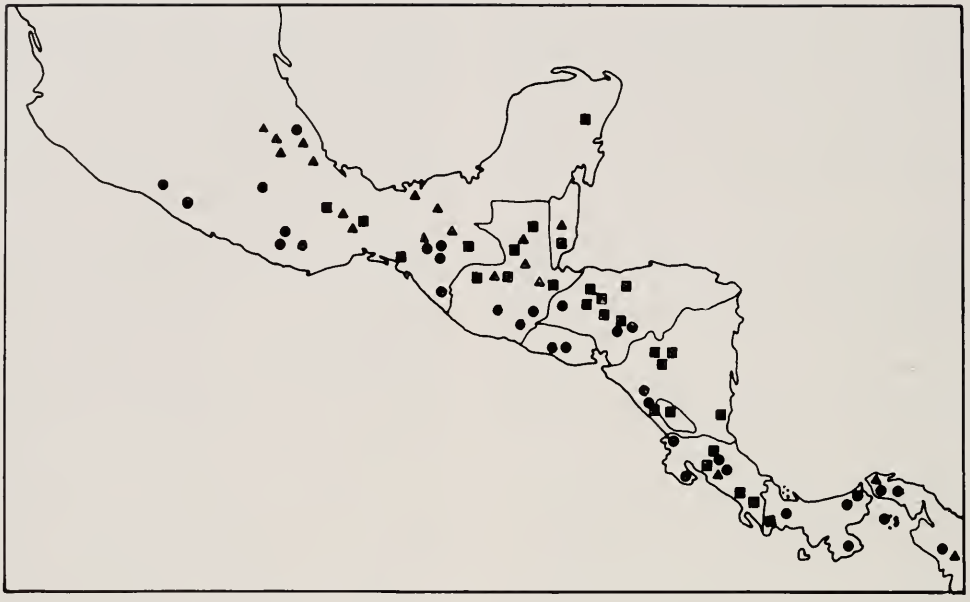

Fig. 18. Distribution of *Begonia nelumbiifolia* (triangles), *B. plebeja* (circles) and *B. sericoneura* (squares).

mens like *Breedlove 35337* from near Palenque, Mexico revealed rudimentary excrescences on pedicels a slight distance beneath the ovary. In other species where such outgrowths were noticed, pistillate flowers with small bracteoles were eventually encountered.

Of several locations cited by Schlechtendal in the original description, only Schiede and Deppe specimens from Misantla were located. I have selected for a lectotype of *B. nelumbiifolia* the sheet of *Schiede 730* at Berlin which best fits the protologue. Both *B. deryckxiana* and *B. caudilimba* are considered to be conspecific with *B. nelumbiifolia*. The relationship between *B. deryckxiana* and *B. nelumbiifolia* was recognized by Alphonse de Candolle (1864) and both *B. deryckxiana* and *B. caudilimba* were included by Smith and Schubert in *B. nelumbiifolia* (1946, 1958, 1961).

Begonia nelumbiifolia is one of four taxa is sect. *Gireoudia* with peltate leaves. It is immediately distinguished from *B. conchifolia* and *B. fonsecae* by its larger leaf blades and petioles and by its ovate, oblong or elliptic dorsal capsule wings. From the few collections of *B. manicata* var. *peltata* available, it appears that this taxon may have leaf blades that approach *B. nelumbiifolia* in size, but *B. manicata* var. *peltata* differs sharply from *B. nelumbiifolia* in its squamose petiolar indument and in its subequal capsule wings. The distinctions between the peltately leaved species are summarized in Table 7. *Begonia nelumbiifolia* has no clear alliances with other Central American species in sect. *Gireoudia*, sharing its rhizomatous habit with all but 5 of the species. Although almost 40 percent of these taxa have petiolar induments formed from whiplash trichomes, *B. nelumbiifolia* stands apart in having whiplash trichomes with sclerenchymatous cores. It also differs from these species in its bicornute stigmas and capsule/primary wing form. In this latter character, *B. nelumbiifolia* appears most

TABLE 7. Morphological comparison of *Begonia nelumbiifolia*, *B. manicata* var. *peltata*, *B. conchifolia* and *B. fonsecae*.

	B. nelumbiifolia	*B. manicata* var. *peltata*	*B. conchifolia*	*B. fonsecae*
Rhizome diameter (mm)	7-28	(6)7-14	(1.5)2.5-6(11)	±15
Leaf blade length (cm)	15-40	(4)7-21.3(27.5)	2-9(14)	13.5-15.5
Petiolar indument	hirsute	squamose	tomentose-lanate	tomentose
Trichome form	basally multiserate whiplash trichomes	scales	basally uniseriate whiplash trichomes	basally multiseriate whiplash trichomes
Staminate sepal length (mm)	4-6	(2.5)3-6(8)	3.5-6.5	6.5-7
Stamen number	13-38(46)	5-10(13)	6-13	27-30
Bracteoles	ebracteolate	ebracteolate	bracteolate	ebracteolate
Ovary length (mm)	4.5-7(8)	4.5-7(8)	7-10	4-6.5
Capsule wing relationship	wings unequal	wings equal to subequal	wings subequal	wings unequal

similar to several poorly known endemic Mexican taxa including *B. karwinskyana* A.DC.

In Mexico *B. nelumbiifolia* has been observed growing in close proximity to several other species in the section. In one area of sympatry with *B. heracleifolia* in Chiapas near Cascadas Agua Azul, several putative hybrids between these taxa were observed and collected (*Utley & Utley 6892*). The suspected hybrids possess large, peltate but pseudocordate, strongly lobed leaves which appear vegetatively intermediate between the large peltate leaves characteristic of *B. nelumbiifolia* and the basifixed, strongly palmately lobed leaves of *B. heracleifolia*.

SPECIMENS EXAMINED: MEXICO: Chiapas: 2-4 km below Ixhuatán along rd to Pichucalco, Municipio of Solosuchiapa, 1200 m, *Breedlove 34881* (DS); rainforest adjacent to small cascading river at Agua Azul, Municipio of Palenque, 300 m, *Breedlove 35337* (DS, MO); hills 20 air km SW of Tenosique, 150-250 m, *Conrad & Conrad 2996* (MO); on limestone rocks and ledges of Misola waterfall, *Hoover 40* (MO); on path from ruins of Palenque to village of Naranja, *Hoover 41* (MO); Palenque, *Liebmann s.n.* (C); about 1 km S of San Miquel on gravel road from Palenque, *McPherson 753* (MICH); near junction of Río Perlas and Río Jataté at San Quintín, *Sohns 1726* (US). Hidalgo: on limestone cliff 42 mi N of Jacala, *Barkley 17M102* (GH); wet mountainside 35 km N of Jacala *Barkley 17M243* (GH); in tropical rainforest 12 mi S of Tamazunchale, *Barkley, Rowell & Webster 7272* (GH); Atlapexco, *Seler & Seler 599* (B); near km 340 on highway below Chapulhuacan, *Moore 2720* (BH, GH, UC, US); slopes by Río San Pedro between Calnali and Huazalingo, *Moore 3023* (BH, GH, UC); near km 340 on highway below Chapulhuacan, *Moore 3409* (BH, GH). Oaxaca: 4.5 mi S Valle Nacional on steep hills above hwy 175 between Tuxtepec and Oaxaca, 430 m, *Croat 39709* (MO); Distrito Choapam, Yavea, Arroyo de San Pedro, steep bank above stream, 450 m, *Mexia 9193* (GH, MO, US); Cuasimulco (Rancho Grande), *Miranda 1139* (MEXU); Belleville, *Orcutt 6346* (US); base of Cerro del Palció, Chiltepec, 300 ft, *Schultes 595* (GH); slopes of Cerro Nariz, Usila, 300 m, *Schultes 667* (GH); Cerro de Lalana, Lalana, near Choapam, 550 m, *Schultes & Reko 810* (GH); San Juan Lalana, 550 m, *Schultes & Reko*

838 (GH, US). Puebla: Presa Mazatepec, camino a Teziutlán, 900 m, *Boege 2760* (MEXU, NY). San Luis Potosí: mountains along route 85, ca. 1 mile N of San Luis Potosí-Hidalgo border, *King 4235* (MICH, NY, UC, US). Tabasco: ripa saxosa fluminis, Teapa, *Rovirosa 574* (US). Veracruz: Orizaba, *Botteri 140* (in part) (GH); Vallee de Córdova, *Bourgeau 2260* (F, LE, MEXU, P); Estación de biologica tropical Los Tuxtlas, San Andres Tuxtla, *Cedillo & Calzada 120* (C); Wartenberg near Tantoyuca, *Ervendberg 261* (GH); Cordillera, without further locality, *Galeotti 198* (P); Municipio Emiliano Zapata: km 368-371 on Jalapa-Veracruz hwy between Cerro Gordo and Plan del Río, *Gilly, Simpson & Dobbs 66* (MICH); Córdoba, *Karwinsky 732* (LE); Colipa, *Liebmann s.n.* (C); Volcán de San Martín, *Nevling & Gómez-Pompa 2539* (GH, MEXU); barranca de Panoaya, *Purpus 8543* (GH, MO, NY, UC, US). Yucatán-Tabasco: without further locality, *Johnson s.n.* (NY). State unknown: Hacienda de Jovo, *Liebmann s.n.* (C). BELIZE. Toledo: Union Camp, *Whiteford 1687* (BM). GUATEMALA. Alta Verapaz: Sebol, high forest S on old road to Petén, *Contreras 4399* (DS, LL); Finca Argentina above Papalha, *Croat 41552* (MO); *Croat 41570* (MO); Cacao, Finca Trece Aguas, 900-1100 ft, *Goll 57* (US); trail to Senahii, *Goll 109* (US); Chama, 900 ft., *Johnston 182* (US); damp thicket, about 360 m, *Standley 70753* (F); near Pancajché, 360 m, *Standley 70772* (F); Pantín, below Tamahú, 600 m, *Standley 70839* (F); damp limestone forest along the Petén Highway, between Campur and Socoyo, 1100 m, *Standley 91717* (F); Río Polochic below Tamahú, 975 m, *Standley 91761* (F); Río Polochic near Pancajché, 900 m, *Standley 91835* (F); vicinity of caves SW of Lanquín, 600-1000 m, *Steyermark 44115* (F, GH); Cerro Chinajá, between Finca Yalpemech and Chinajá, 150-700 m, *Steyermark 45557* (F, GH); about 4 km from Finca Pansamala, *Stuart 1* (MICH). Izabal: Lago Izabal, 1-5 km from highway CA-9 on rd to Mariscos, 0-600 m, *Jones, Proctor & Facey 3125* (F, NY); gorge of Río Sauce, El Boquerón, 3-5 mi N of Lake Izabal, E of El Estor, 10-20 m, *Jones & Facey 3452* (F, LL, NY); between Milla 49.5 and ridge 6 mi from Izabal, Montaña del Mico, 65-300 m, *Steyermark 38624* (F); Río Dulce, 2-4 mi W of Livingston, on S side, 1-3 m, *Steyermark 39519* (F); along Río Frio on rocky limestone bluffs, *Steyermark 41605* (F, GH). Petén: Dolores, Río Santo Toribio trail about 3 km NW in high forest, *Contreras 2431* (LL); Lacandon, low forest bordering lake, about 3 km N, *Contreras 3541* (LL, MO, US); foresta baja, en orillando el camino para Poctún, at km 25, *Tun Ortiz 1082* (BM, F, NY, US). COSTA RICA: Alajuela: Río Cacao, 800 m, *Gómez 19567* (NOLS). PANAMA: Darién: banks of Río Paca, *Stern et al. 708* (GH, MO, US); Caña-Cuasi Trail (Camp 1), Chepyana, *Terry & Terry 1623* (F, GH). Panamá: Ipetí, base of Serrannia de Maje, *Folsom & Lantz 1915* (MO); without locality, *Seemann 1098* (BM). COLOMBIA. Antioquia: cerca Villa Arteaga, 150 m, *Gutierrez & Barkley 18C549* (US); humid region below D'Abeiba, *Barkley & Gutierrez-Villigas 35437* (US). Bolivar: Boca Verde on Río Sinu, *Pennell 4577* (US).

15. *Begonia thiemei* C.DC., Bot. Gaz. 20: 542. 1895. TYPE: HONDURAS: Santa Bárbara: San Pedro Sula, 800 ft, March 1888. *Thieme 5240* (Holotype: G!; isotypes: G!, US!).

    Begonia macdougallii Ziesenhenne, The Begonian 14: 220. 1947. TYPE: MEXICO: Chiapas: Cerro Carrizal, Rancho Aguajito in Ocozocoautla rain forest, *MacDougall C-40* (Holotype: Herbarium Ziesenhenne, n.v.; isotype: US!).

Herbaceous perennials; *rhizomes* repent, often branching with age, 8-30 cm long; internodes 1-2 X 0.7-2.3 cm, lenticellate and glabrous. *Leaf blades* palmately compound with 7-10 leaflets, chartaceous to membranaceous, oblique, suborbicular to broadly ovate, 21-54 X 20-39 cm, glabrous or occasionally sparsely hirtellous above and glabrous in intercostal regions but sparingly pilose on primary nerves beneath; leaflets straight to subfalcate, asymmetrically narrowly elliptic, lanceolate or obovate-oblanceolate, (10) 17-32 X 1.6-7 (10) cm, basally oblique to cuneate, apically acuminate to attenuate-acuminate or rarely deeply bilobed to half the leaflet length, marginally occasionally with a broad acuminate lobe near the leaflet apex, often serrate opposite major nerves, irregularly serrulate and frequently ciliate. *Petioles* 36.5-62 cm X 2.5-13 mm, lenticellate, glabrous to very sparsely pilose or glandular-pilose; petiolules 1.1-4.5 cm long, glabrous. *Stipules* fugacious, succulent but becoming scarious when dry, subnavicu-

lar, asymmetrically broadly ovate to triangular, 1.2-1.9 X 0.6-1.9 cm, weakly keeled, apically acute, marginally entire. *Inflorescences* greatly exceeding the leaves, strongly asymmetric to unilateral, laxly cymose, few- to many-flowered, 15-22 cm diam. *Peduncles* to 85.5 X 0.7-1.7 cm, glabrous to sparsely pilose. *Bracts* fugacious, not seen. *Staminate flowers*: pedicels 8-13 mm long: sepals white to green-white or yellow, broadly ovate to suborbicular or transversely broadly elliptic, 7-9 (13) X 8-11 (14) mm, glabrous to glandular externally; petals wanting; stamens 21-27 (36); filaments 0.1-1.2 mm long, inserted on a short torus; anthers narrowly obovate to oblanceolate, 2-3.1 X 0.6-1 mm. *Pistillate flowers*: pedicels 7-11 mm long; bracteoles wanting; sepals colored like staminate sepals, ovate or obovate, 5-7 X 6-7 mm, glabrous to glandular externally; petals wanting; ovary 6-10 mm long, often sparsely glandular, styles 3, 1.5-2 mm long, connate only briefly basally; stigmas broadly lunate, weakly spiralling at the ends. *Capsules* with pedicels (14) 16-23 (30) mm; trilocular, 8-16 mm long; locule chambers externally appearing ovate, oblong or suborbicular, 6.5-11 X 6-11 mm; wings 3, unequal, the largest variable, asymmetric or occasionally subfalcate, ovate to elliptic, 10-21 X 8-20 mm, apically obtuse to subacute, the second asymmetrically lunate to lunate-triangular, 5-10 X 7-12 (14) mm, the third marginiform or subequal to the second.

DISTRIBUTION AND HABITAT: Veracruz and Chiapas in southern Mexico to northern Honduras at elevations between 50-2000 m. The type, *Thieme 5240,* is the only collection of this species known from Honduras. With the exception of *Steyermark 49188* which was gathered between 1200-2000 m, all other collections of this taxon were from 50-800 m elevation. This species colonizes steep forested slopes, rocky areas near streams and occasionally road banks in both wet primary and secondary forests. (Fig. 12).

FLOWERING: Flowering specimens have been collected from March to May.

DISCUSSION: *Begonia thiemei* may be distinguished by its glabrous or sparsely pubescent, palmately compound leaves, asymmetric cymes, yellow to greenish white or white sepals and large, narrowly oblong-obovate to oblanceolate anthers. While this species typically has bright green leaves, one population in southern Mexico was observed in which a deep maroon leaved form grew intermixed with the typical green form (pers. observation).

Casmir de Candolle (1895) described *B. thiemei* as having herbaceous stems with clustered, oblong, pinnately nerved leaves. Careful examination of both the holotype from Geneva (G) and the isotype at U.S. National Herbarium (US) revealed that this taxon has palmately compound leaves with penninerved, lanceolate leaflets. Only a few other *Begonia* species possess this unusual leaf form, including *B. carolineifolia* Regel (sect. *Gireoudia*) from Mexico and *B. hemsleyana* Hook. f. (sect. *Petermannia* (Kl.) A.DC) from China. Early collections of *B. thiemei* from Guatemala were referred by Smith and Schubert to *B. carolineifolia* probably because of striking similarities in leaf form between the species. Although both taxa are rhizomatous, *B. thiemei* has a repent rhizome, while *B. carolineifolia* has a fleshy erect or ascending rhizome similar to the rhizomes characteristic of *B. sericoneura, B. crassicaulis* and *B. cardiocarpa. Begonia thiemei* also differs from *B. carolineifolia* in its sparse petiolar indument of villi, larger staminate sepals (7-9 [13] X 8-11 [14] vs. 4-6 X 6.5-8 [9] mm), more numerous stamens (21-27 (36) vs. 13-19)

and larger anthers (2-3.1 vs. 1-1.7 mm). Based upon a number of misidentified collections of *B. thiemei,* Smith and Schubert (1961) included *B. carolineifolia* in their treatment of the Begoniaceae for the Flora of Guatemala. As *B. carolineifolia* is presently interpreted, it is restricted to the states of Oaxaca and Veracruz in southern Mexico.

Houghton (1924), in an unpublished dissertation, placed *B. thiemei* in sect. *Ruizopavonia* because of its seemingly penninerved, lanceolate leaves. He also proposed another species in sect. *Ruizopavonia, B. lancifolia* that was never published, based on a specimen consisting of only leaf fragments and portions of an inflorescence, *Watson 417* (GH). This material is treated here as *B. thiemei. Begonia thiemei* has been widely cultivated since its introduction into horticulture as *B. macdougallii.* Although the holotype of *B. macdougallii* was unavailable for study, from Ziesenshenne's description and a leaf fragment of *B. macdougallii* in the U.S. National Herbarium, it is obvious that *B. macdougallii* is conspecific with *B. thiemei.*

Since *B. thiemei* is one of the larger species in sect. *Gireoudia,* it is not surprising that specimens commonly lack rhizomes and complete petioles and peduncles. Flowering specimens apparently may reach 2.5 m high (*fide Schubert, Gómez-Pompa & Rojas 1848*), yet the largest peduncle observed on a specimen was only 89.5 cm (*Steyermark 39148*). It is also likely that leaves of convenient size are often selected by collectors. Considering these factors it is apparent that for many characters in *B. thiemei,* the magnitude of the variability remains poorly known and *B. thiemei* must await more thorough collection before it can be adequately evaluated.

SPECIMENS EXAMINED: MEXICO. Chiapas: SW side of Prensa de Malpaso, Municipio of Ocozocoautla de Espinosa, 2200 ft., *Shilom Ton 3771* (DS, US). Veracruz: estación biologica, Los Tuxtlas, 170 m, *Martínez-Calderón 2258* (A, CAS, F, MEXU, MICH, US); Sontecomapa, roadside near San Andres Tuxtla, *Schubert, Gómez-Pompa & Rojas 1848* (US). GUATEMALA. Huehuetenango: Cerro Chiblac, between Finca San Rafael and Ixcán, Sierra de los Cuchumatanes, 1200-2000 m, *Steyermark 49188* (F, GH); Cerro Victoria, across river from Finca San Rafael, Sierra de los Cuchumatanes, 800 m, *Steyermark 49641* (F). Izabal: Río Juyamá, SE of Cheyenne, about 15 mi SW of Bananera, 50-100 m, *Steyermark 39148* (F). Verapaz and Chiquimula: eastern portion, without further locality, *Watson 417* (GH).

16. *Begonia manicata* Brongn. ex Cels, Jour. Jard. (Ann. Fl. et Pom.) 104. f. 257. 1842.

Acaulescent or caulescent herbs; *rhizomes* often repent when young, soon becoming erect to suberect, 0.4-20 dm long; internodes very short to elongate, (0.3) 1.1-3.5 cm X 6-14 mm, glabrous throughout or infrequently glandular or very sparingly squamose. *Leaf blades* simple, oblique to transverse, asymmetric, variable in form, ovate, oblong-elliptic, obovate or infrequently suborbicular, 7.9-25.5 (32.5) X (4) 7-21.3 (27.5) cm, basally cordate or rarely peltate, apically attenuate-acuminate or abruptly acuminate, but infrequently acute to obtuse, marginally ciliate, obsoletely to moderately undulate, often dentate or broadly but shallowly lobed at ends of major nerves but rarely deeply lobed opposite the petiole insertion, ciliate-denticulate, nitidous and glabrous throughout above but glabrous in intercostal regions and sparingly squamose with broad lacerate scales 4.5-6 (7) mm long on principal nerves beneath, (7) 8-9 (11)-palmatinerved or rarely 9-peltinerved. *Petioles* (4.7) 12.3-22.6 (25) cm X 1.5-3 (6) mm, sparingly to densely squamose throughout, or rarely only distally, but especially pronounced distally with one or more dense concentric rings of scales character-

istically present, indument often consisting of deep, broad lacerate scales 2-7 (10) mm long occurring singly or in groups 2 to many trichomes long and one trichome wide. *Stipules* deciduous, ascending but spreading to reflexed with age, narrowly triangular to narrowly or broadly ovate, 1.1-2.6 X (0.5) 0.7-1.4 cm, strongly keeled, apically acute to acuminate, marginally entire, glabrous but the keel frequently fimbriate or lacerate. *Inflorescences* generally exceeding or greatly exceeding the foliage, moderately to strongly asymmetric, usually many-flowered, (3.5) 11-29 cm diam. *Peduncles* (6) 14.5-32.5 (48) cm X 1.5-7 (11) mm, glabrous or rarely sparingly squamose. *Bracts* caducous, the lowermost ovate to oblong or obovate, (9.5) 11-13 X 4.5-8 mm, apically subacute, marginally entire or rarely weakly denticulate basally. *Staminate flowers*: pedicels (3) 4-10 mm long; sepals white to light pink, narrowly ovate, weakly obovate to broadly elliptic or suborbicular, (2.5) 3-6.5 (8) X 3-5 (7.5) mm, glabrous; petals wanting; stamens 5-10 (13); filaments (0.3) 0.4-1 mm long, borne on a raised torus; anthers narrowly oblong or subelliptic to obovate, (0.8) 1-1.5 X 0.5-0.9 (1) mm. *Pistillate flowers*: pedicels (4) 5-10 mm long; bracteoles wanting or obsolete; sepals colored like staminate sepals, obovate to suborbicular, 3.5-5.5 (6) X (2.5) 3-4.5 mm, glabrous; petals wanting; ovary (7) 8.5-11 mm long, glabrous; styles 3, 1.5-2 mm long, connate 1/4-1/2 their length; stigmas lunate. *Capsules* with pedicels 7-11 mm long, trilocular, (5.5) 7-12 (13) mm long; locule chambers externally appearing oblong to subelliptic, broadly elliptic or weakly obovate, 5.5-7 (8) X 3.5-5.5 mm; wings 3, forming broad longitudinal bands from the capsule apex to the pedicel, equal to subequal, the largest broadly but shallowly asymmetrically triangular or lunate-triangular, 4.5-6.5 (8) X 8-12 mm, apically obtuse to subacute, the second and third equal or subequal to first, shallowly asymmetrically triangular to sublunate, 4.5-6.5 X 8-11.5 mm.

DISCUSSION: *Begonia manicata* is at once distinguished from other Central American species in sect. *Gireoudia* by its squamose petiolar indument which typically forms several dense, concentric rings on the petiole just beneath the petiole-leaf blade junction and its equal or subequal capsule wings.

Although other species in the section have squamose induments, *B. manicata* is the only taxon with erect or ascending rhizomes and squamose petioles. Only three other Central American species have rhizomes similar to *B. manicata*, *B. cardiocarpa*, *B. crassicaulis* and *B. sericoneura*, but *B. manicata* is quickly distinguished from the latter two taxa by its squamose indument, while *B. crassicaulis* and *B. sericoneura* have dense induments of fine sericeous whiplash trichomes. *Begonia manicata* differs markedly from *B. crassicaulis* in leaf blade form which is asymmetric with unlobed or rarely irregularly lobed margins in *B. manicata*, but symmetric with deeply palmately lobed margins in *B. crassicaulis* Stamen number is lower in *B. manicata* than in most other species in sect. *Gireoudia* and the lowest counts obtained in this taxon (5) are also the lowest reported for sect. *Gireoudia*. Leaf margination is somewhat variable in *B. manicata* with specimens from the northern parts of its range regularly having only undulate to dentate margins while specimens from Nicaragua and Honduras have irregularly shallowly lobed margins.

Begonia manicata is phenetically most similar to *B. cardiocarpa* with which it shares a similar erect or ascending rhizomatous habit, sepal shape and size, lunate stigmas and equal to subequal cap-

sule wings. These species differ in their internodal indument which is wanting or rarely sparsely squamose in *B. manicata* but coarsely villous with barbate trichomes in *B. cardiocarpa*. While the petiolar indument of *B. manicata* is squamose, in *B. cardiocarpa* it consists of whiplash and barbate trichomes. Stamen number also differs between the taxa, with *B. manicata* typically having 5-10 (13) stamens while *B. cardiocarpa* is characterized by (12) 16-32 (37) stamens. Bracteoles are rudimentary or wanting in *B. manicata* but are conspicuous on flowers of *B. cardiocarpa* (Table 8).

Two morphological forms are presently recognized in *B. manicata*, *B. manicata* var. *manicata* and var. *peltata* which differs from the typical varient in having peltate leaves. Because of scant material, it was impossible to determine the nature and variation of many other characters in *B. manicata* var. *peltata*. Until more material is available, var. *peltata* is best maintained as distinct. As such it is the only known peltately leaved form of an otherwise non-peltate species in sect. *Gireoudia*.

Key to the Varieties of *B. manicata*

Leaves basally cordate; palmatinerved ..... var. *manicata*

Leaves basally peltate; peltinerved ..... var. *peltata*

Begonia manicata var. *manicata*

Begonia manicata Brongn. ex Cels, Jour. Jard. (Ann. Fl. et Pom.) 104. f. 257. 1842. TYPE: without locality (Holotype: not seen and perhaps non-existent).

Begonia schizolepis Liebm., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1852: 17. 1852. TYPE: MEXICO: Veracruz: March 1842. *Liebmann s.n.* (Lectotype: C!; isolectotypes: C!, P!).

Begonia lepidota Liebm., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1852: 17. 1852. TYPE: NICARAGUA: in prov. Segovia. In monte Pantasmo, 4500 ft, January 1842, *Oersted s.n.* (Holotype: C!).

Gireoudia manicata (Brongn. ex Cels) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

Gireoudia schizolepis (Liebm.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

Begonia robustior Standl. & L. Wms., Ceiba 1: 155. 1950. TYPE: HONDURAS: Olancho: trail between Catacamas

TABLE 8. Character differences between *Begonia cardiocarpa* and *B. manicata*.

	B. cardiocarpa	*B. manicata*
Internodal indument	villous	glabrous or rarely sparingly squamose
Trichome type	whiplash trichomes and coarse barbate trichomes	lacerate scales
Petiolar indument	villous	squamose
Trichome type	whiplash and barbate trichomes	broad lacerate scales
Stamen number	(12) 16-32 (37)	5-10 (13)
Bracteoles	poorly developed	wanting to obsolete

and La Presa, N of Catacamas, 500-600 m, March 20-25, 1949, *Standley 18516* (Holotype: US!; isotype: F!).

Leaf blades asymmetric, variable in form, ovate, oblong-elliptic, obovate or suborbicular, basally cordate; palmatinerved.

DISTRIBUTION AND HABITAT: Southern Mexico to Nicaragua, from 200-1800 m elevation. *Begonia manicata* is frequently saxicolous and is common on limestone outcrops throughout its distribution (Fig. 19).

FLOWERING: November-April.

DISCUSSION: Included in *B. manicata* var. *manicata* are *B. lepidota* and *B. schizolepis* which were first treated as synonymous with *B. manicata* by Candolle (1864). I have selected a lectotype for *B. schizolepis*, the Liebmann collection at Copenhagen that was gathered in Veracruz, Mexico in March 1842, from the many specimens of this taxon collected by Liebmann. *Begonia manicata* var. *manicata* also encompasses *B. robustior* with which it agrees in all critical features.

SPECIMENS EXAMINED: MEXICO. Chiapas: lower montane rain forest 13 km N of Berriozábal near Pozo Turipache and Finca El Suspiro, Municipio of Berriozábal, 900 m, *Breedlove 24826* (DS). Oaxaca: along rd between Teotitlán del Camino and Chichotla, 1265 m, *Croat 48353* (MO); *Croat 48393* (MO); Chichotla, Huautla de Jiménez, 1350 m, *Matuda 38606* (CAS). Puebla: Texcaco, 1200 m, *Gold 11* (US); Guachinango, *Matuda 29383* (US). Veracruz: environs de Orizaba, *Botteri & Sumichrast 1670* (P); Córdoba, *Bourgeau 1983* (GH, MEXU, P); *Bourgeau 1985* (F, M, NY, US); *Bourgeau 1987* (GH, US); *Galeotti 198* (K); Orizaba, *Gray s.n.* (GH, USF); Barranca de Coscomatepec, *Liebmann s.n.* (C); Mirador, *Liebmann s.n.* (C, UC); *Liebmann s.n.* (C); *Liebmann s.n.* (B); Rio Jamapa sobre el Camino Calcahualco a Coscomatepec, 1600 m, *Lot 1191* (CAS, F, GH, MEXU); Barranca de Texolo between Coatepec and Teocelo, 1100 m, *Moore 6276* (BH, MEXU, UC, US); Barranca de Tenampa, Zacuapan, *Purpus 2919* (MO); Zacuapan, *Purpus 3686* (B, F, GH, MO, NY, UC, US); moist rocks without further locality, *Purpus 6353* (GH, MO, NY, UC); Zacuapan, *Purpus 6622* (UC); *Purpus 7131* (UC); Cerro de Chiahuaxtla-Cuauhtlapan, 1600 m, *Rosas 1033* (CAS, GH, MEXU); Barranca

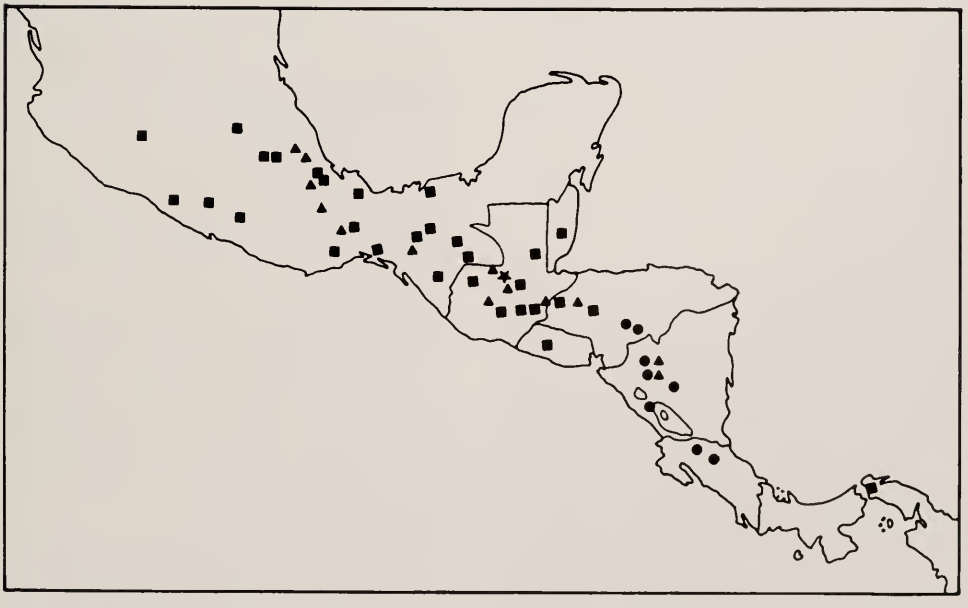

Fig. 19. Distribution of *Begonia cardiocarpa* (circles), *B. heracleifolia* (squares), *B. manicata* var. *manicata* (triangles) and *B. manicata* var. *peltata* (stars).

de Tioselo, *Schiede s.n.* (B); El Cajón, Municipio de Yecuatla, 1100 m, *Ventura 4810* (MICH, P, WIS); La Barranca, Municipio of Coscomatepec, 1250 m, *Ventura 5036* (MICH); Esquilón, Municipio of Jilotepec, 1400 m, *Ventura 7664* (MICH); Coscontla, Municipio de Huatusco, 1400 m, *Ventura 7965* (CAS, MEXU, MICH); Xico, Cascades de Texolo, 30 km W of Xalapa, 1100 m, *Wilkening 28* (WIS). Without locality, *Liebmann s.n.* (US); *Sesse et al.* (F). GUATEMALA: Alta Verapaz: between San Pedro Carchá and Campus, 1200-1350 m, *Harmon & Fuentes 2164* (F, GH, MO); lime rocks in woods near Cobán, 4000 ft, *Hunnewell 17176* (GH); *Hunnewell 17177* (GH); bosque mixto de Chamal, 1200 m, *Molina & Molina 12155* (F, NY); Quiché Hwy about 12 km W of San Cristóbal, 1100 m, *Standley 89747* (F); *Standley 89756* (F); ravine along Río Carchá between Cobán and San Pedro Carchá, 1360 m, *Standley 90034* (F); *Standley 90109* (F); *Standley 90127* (F, GH); *Standley 90153* (F); Cobán 1300 m, *Standley 90907* (F); *Standley 91541* (F); damp forest between San Cristóbal Verapaz and Chixoy, 1200-1300 m, *Steyermark 43916* (F, GH); Cobán, 1350 m, *von Türckheim II 1872* (US); hills about 8 km SE of Cobán, 1500 m, *Williams et al. 40277* (BM, F); wet mossy limestone, valley 1-5 km E of San Juan Chamelco, 1500-1600 m, *Williams, Wilson & Freeze 40474* (F); Río Cobán, E of Cobán, 1300 m, *Williams et al. 40634* (F, NY, US); *Williams et al. 43641* (F, MICH, US). Chiquimula: Volcán Ipala, 900-1510 m, *Steyermark 30507* (F); rocks at summit of Montaña Nonojá in cloud forest, 3-5 mi E of Camotán, 600-1800 m, *Steyermark 31707* (F). Zacapá: Rillito del Volcán de Monos, Volcán de Monos, 1150-2100 m, *Steyermark 42380* (F, GH, US). HONDURAS: Morazán: cleared pine forest near Rosario Mine, San Juancito Mountains, 1500 m, *Morton 7364* (US); Chahuité, 800-1075 m, *Standley, Molina & Chacon 5016* (F). Santa Bárbara: limestone ridges on forested slopes of Cerro Santa Bárbara, rd to Mochito Mine, 1500 m, *Allen 6377* (F, GH, US). Department unknown: montane forest between Cofridiá and Rancho Quemada, *Barkley & Errazuriz 40310* (GH). NICARAGUA: Jinotega: cloud forest along Hwy 3 from Jinotega to Matagalpa, 5-8 km SW of Jinotega, 1500 m, *Croat 43051* (MO); cloud forest area between Sta. Lastenia and Sta. Martha, above Jinotega, Cordillera Central de Nicaragua, 1400 m, *Molina & Williams 20068* (F, NY, US); cloud forest along Hwy 3 ca 1.9 km NW of Aranjuez rd entrance, *Stevens 5604* (BM, MO); montane rain forest or cloud forest, Ocotillo near Sta. Lastenia, 1550 m, *Williams et al. 27837* (F, NY, US). Madriz: cutover cloud forest area on Volcán Somoto, *Molina & Williams 20242* (F, NY). Matagalpa: wet dense forest between El Triunfo and Fuente Pura, above Santa María de Ostuma, 1800 m, *Molina 20404* (F); cut-over cloud forest area El Porvenir, Cordillera Central of Nicaragua, 1700 m, *Molina 20553* (F, NY); premontane moist and lower montane wet forest, Hacienda Santa María de Ostuma, Cordillera Dariense, 1300-1600 m, *Tomlin 165* (MO); cloud forest area, Sta. María de Ostuma, Cordillera Central between Matagalpa and Jinotega, 1300-1500 m, *Williams, Molina & Williams 23393* (F); *Williams, Molina & Williams 23409* (F, US); *Williams, Molina & Williams 24640* (F,); *Williams, Molina & Williams 24690* (F, US).

Begonia manicata var. *peltata* Smith & Schubert, Field Mus. Nat. Hist. Bot. 24: 175. 1961. TYPE: GUATEMALA: Alta Verapaz, Montaña Yxocubvain, 2.5 mi W of Cubilquitz, 300-500 m, March 12, 1942. *Steyermark 44980* (Holotype: GH!)

Leaf blades asymmetric, variable in form, ovate, oblong-elliptic or suborbicular, basally peltate, peltinerved.

DISTRIBUTION AND HABITAT: Known only from Alta Verapaz, Guatemala (Fig. 19).

FLOWERING: March.

DISCUSSION: *Begonia manicata* var. *peltata* differs from the other peltately leaved taxa in sect. *Gireoudia* in its conspicuously squamose petiolar indument and its equal capsule wings. The salient features separating these taxa are summarized in Table 7.

ADDITIONAL SPECIMENS EXAMINED: GUATEMALA: Alta Verapaz: high forest S of Cobán Rd, *Contreras 4339A* (LL).

17. *Begonia cardiocarpa* Liebm., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1852: 13. 1852. TYPE: NICARAGUA: Segovia: In monte Pantasmo, 4500 ft, February 1848. *Oersted s.n.* (Holotype: C!; isotype: B!).

Gireoudia cardiocarpa (Liebm.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

Begonia bakeri C.DC., Bull. Herb. Boiss. II. 8: 320. 1908. TYPE: NICARAGUA: Granada: Volcán Mombacho, February 10, 1903, *Baker 2333* (Holotype: G!; isotypes: K! [2 sheets], MO!, NY!, US!).

Acaulescent or caulescent herbs; *rhizomes* fleshy, green but becoming silvery gray with age, often repent or procumbent when young, but with age erect to semi-erect and with further elongation becoming declined and eventually decumbent, then rooting where in contact with the substrate and re-establishing an upright posture, short becoming elongate with age, 0.3-15 dm long; internodes short to elongate, (0.5) 0.9-2.3 X 0.6-1.4 (1.8) cm, moderately to densely villous, with an indument of whiplash trichomes intermixed with coarse, narrow barbate, basally rounded or flattened trichomes 2-6 mm long, these occasionally forming a band nodally around the petiole base. *Leaf blades* simple, oblique to transverse, narrowly ovate to oblong or infrequently suborbicular, (5.5) 7-21 (30) X (3.2) 5-13 (21.5) cm, basally broadly shallowly cordate to narrowly deeply cordate with lobes occasionally overlapping, apically broadly long attenuate-acuminate, marginally often doubly dentate to doubly serrate, frequently obsoletely undulate or broadly lobed with one or more lobes, but the principal lobe opposite the petiole insertion, apically lobes acute to attenuate-acuminate or obtuse, ciliate-denticulate to ciliate-serrulate and ciliate, glabrous throughout or infrequently sparingly pilose basally on principal nerves above and glabrous to sparingly pilose in intercostal regions but sparsely to moderately pilose on principal nerves beneath, palmately (6) 7-8-nerved. *Petioles* light green, but often deep red at bases of trichomes, (2) 4-19 (31) cm X (0.5) 1-4 mm, sparingly to moderately villous throughout, often with minute glandular trichomes interspersed, but indument often most dense distally with trichomes often clustered and frequently basally connate, forming oblique to transverse bands 2-8 trichomes long and 1 trichome wide, the whiplash or infrequently barbate basally rounded or flattened trichomes translucent white distally but deep red basally, 2-4 mm long. *Stipules* deciduous, translucent light green but when dry, pale cinnamon or ferrugineous with darker nerves and hyaline intercostal regions, subnavicular especially distally, asymmetric, triangular to broadly lanceolate-subovate, 1-3.2 X 0.6-1.8 cm, strongly keeled, apically acute to acuminate, marginally entire, glabrous or hirsute throughout, but the keel commonly lacerate and fimbriate. *Inflorescences* generally greatly exceeding the foliage when mature, weakly to moderately asymmetric, many-flowered, 6-30 cm diam. *Peduncles* light green, (4.5) 15-40 (45) cm X 1-8.5 mm, glabrous, glandular, sparingly pilose or glandular-pilose throughout. *Bracts* caducous, light green, the lowermost equitant in bud, navicular, elliptic to ovate or obovate, (4-5) 7-12 (22) X (3.5) 4-8.5 (13) mm, weakly keeled especially distally, apically obtuse, marginally ciliate-denticulate to ciliate-serrulate, glabrous except for the fimbriate-pilose keel. *Staminate flowers*: pedicels 6-14 mm long; sepals white to light pink, suborbicular, ovate or obovate, (4) 5-8 (9) X (3.5) 4.5-8 (9) mm, glabrous; petals wanting; stamens (12) 16-32 (37); filaments 0.5-1.5 (1.8) mm long, borne on a raised torus; anthers oblong-obovate to narrowly elliptic, 1-1.5 (1.7) X 0.5-0.8 mm. *Pistillate flowers*: pedicels 4-18 mm long; bracteoles caducous but often present at anthesis, poorly developed, white to light pink, subequal, oblanceolate-obovate, (1) 2-4

(5) X 0.5-2.5 mm, apically acute to obtuse, marginally sparingly ciliate-serrulate, glabrous; sepals colored like staminate sepals, broadly elliptic to suborbicular, infrequently ovate or obovate, 4-6.5 X 4-6 (8) mm, glabrous; petals wanting; ovary white, pink or light green, 7-11 mm long, glabrous or sparingly glandular throughout; styles 3, 1.5-2 mm long, connate to 2/3 their length; stigmas lunate. *Capsules* with pedicels (10) 14-20 (24) mm long, trilocular, 12-14 (16) mm long; locule chambers externally appearing oblong to subelliptic, (7) 9-10.5 X 5-7 mm; wings 3, equal or subequal to one another, forming broad longitudinal bands from capsule apex to pedicel, the largest asymmetrically broadly but shallowly triangular to broadly lunate or sublunate, 4.5-6.5 (8) X 8-12 mm, apically obtuse or subacute, the second and third equal or subequal to the first wing, shallowly asymmetrically triangular to sublunate, 4.5-6.5 X 8-11.5 mm.

DISTRIBUTION AND HABITAT: *Begonia cardiocarpa* ranges from southern Honduras to northern Costa Rica at elevations between 500-1500 m in primarily cloud forest formations and premontane wet forests where it occurs on steep forested slopes and roadbanks. In Costa Rica *B. cardiocarpa* is often epiphytic, growing on the lower trunks of trees in recently disturbed primary forests in the vicinity of Parque Nacional Santa María (Fig. 19).

FLOWERING: Peak flowering occurs between December and March.

DISCUSSION: *Begonia cardiocarpa* is characterized by its succulent, upright rhizomes, densely villous internodes, indument of coarse whiplash trichomes, 12-27 stamens, bracteolate pistillate flowers, lunate stigmas and equal to subequal capsule wings which form broad longitudinal bands along the capsule margin.

With only limited material available for study, Smith and Schubert (1946b, 1961) treated *B. cardiocarpa* as a synonym of *B. sericoneura* (*B. lindeleyana* sensu Smith and Schubert) which it superficially resembles in rhizome form, internode indument and stipules. Recent collections have remained undetermined or have been misidentified as *B. plebeja* but not *B. sericoneura,* indicating Smith recognizes the significant differences existing between the element forming *B. cardiocarpa* and the latter taxon. Among the numerous characters which distinguish *B. cardiocarpa* from *B. sericoneura* are its villous petiolar indument of coarse barbate and whiplash trichomes, glabrous adaxial leaf surface, fewer stamens, bracteole size and shape, small capsules, equal or subequal capsule wings and wing size and shape.

Begonia bakeri, which Casmir de Candolle (1908) described as having entire placentae, is considered to be conspecific with *B. cardiocarpa.* An examination of the holotype and isotypes failed to substantiate Candolle's observation on the placentae, but did reveal that the placentae, while bipartite, possess strongly unequal lobes, which may have contributed to Candolle's erroneous interpretation. Utilizing Candolle's characterization of placentae, Houghton (1924) described sect. *Auriformia* to accomodate *B. bakeri,* but the section remained unpublished until Ziesenhenne (1974) resurrected Houghton's description. Although the type is clearly synonymous with *B. cardiocarpa,* sect. *Auriformia* is identical in salient features to sect. *Haagea* (Kl.) A.DC. from the Far East.

The petiolar indument of *B. cardiocarpa* consists of coarse barbate basally rounded or flattened trichomes frequently intermixed with coarse whiplash trichomes. The trichomes often are aggregated into narrow oblique to transverse bands one trichome wide and several

to many trichomes long. In this condition, adjacent trichomes are usually weakly connate basally. While the trichome bands are distributed throughout the petiole, they are characteristically most dense near the petiole apex. When these bands are well-developed near the petiolar apex, the leaves of *B. cardiocarpa* resemble those of *B. manicata* whose petioles characteristically have dense, concentric rings of broad scales near the petiole apex. The relationship between *B. cardiocarpa* and *B. manicata* is explored in the discussion of *B. manicata* and salient features are summarized in Table 8.

In Costa Rica *Begonia cardiocarpa* occurs sympatrically with *B. sericoneura* in Santa María National Park and in Nicaragua it is potentially sympatric with *B. manicata* near Santa María de Ostuma in the Cordillera Central.

SPECIMENS EXAMINED: HONDURAS. El Paraíso: trail, Danlí to Finca Sta. Emilia, *Carlson 2532* (GH, US); *Carlson 2547* (in part) (MICH); Montaña Apauhis, cerca Danlí, 1000 m, *Molina 7450* (F); Montaña de Cifuentes entre El Urraco y Cifuentes, 900 m, *Molina 11403* (F, LL, NY, US). NICARAGUA. Chontales: Santa Domingo, near summit of Peña Blanca, 800-850 m, *Bunting & Licht 1200* (F, NY, US); 2.8 km N of Cuapa in forest, 400-500 m, *Vincelli 90* (MO). Granada: upper slopes of Volcán Mombacho along W shore of Lake Nicaragua, 1100 m, *Croat 39132* (MO); E side of Volcán Mombacho above Finca Las Delicias, *Hall & Bockus 7569* (MO). Jinotega: Jinotega, 1030-1300 m, *Standley 10071* (F). Matagalpa: moist bank at Santa María de Ostuma, Cordillera Central de Nicaragua; 1400 m, *Molina & Williams 20111* (F, NY, WIS, US); wet forest, La Zopilota, 2 km S of Santa María de Ostuma, 1300 m, *Molina 20452* (NY); vicinity of El Porvenir, 4 km E of Santa María de Ostuma, 1500 m, *Molina 22873* (F, MO, NY); Cañada Yasita, *Rothschuh 322* (B); along Route 5 toward Tuma, 500-1000 m, *Seymour 4047* (MO); *Williams 24038* (F); Sta. María de Ostuma, 1300-1500 m, *Williams, Molina & Williams 23592* (F, US); *Williams, Molina & Williams 24645* (F); cloud forest area N of Sta. María de Ostuma along rd to La Fundadora, 1300-1500 m, *Williams, Molina & Williams 24895* (F, LL, NY, US). Zelaya: trail from Cerro El Inocente toward Cerro Saslaya near source of Caño Majagua, 1050-1150 m, *Stevens 6707* (MO). COSTA RICA. Alajuela: Santa María National Park, 600-900 m, *Liesner 4556* (CR, MO); *Liesner 5112* (MO); *Liesner 5206* (MO); cloud forest zone, Guadalupe, Canton Alfaro Ruiz, 1500 m, *Smith P2201* (US); Camino Santa María 27.6 km NE of Liberia, 800 m, *Utley 5917* (B, C, CR, DUKE, G, MEXU, MO, US).

18. *Begonia heracleifolia* Schlecht. & Cham., Linnaea 5: 603. 1830. TYPE: MEXICO. Hacienda de la Laguna, Baranca de Tioselo, 1828. *Schiede 720* (Holotype: B!).

    Begonia radiata Graham, Edinb. Phil. Jour. 1833: 182. TYPE: described from cultivated material at the Edinburgh Botanic Garden from Berlin (Holotype: not seen and perhaps nonexistent).

    Begonia heracleifolia var. *punctata* Cels, Jour. Jard. 104. 1842. TYPE: described from cultivated material (Holotype: not seen and perhaps nonexistent).

    Begonia jatrophifolia Cels, Jour. Jard. 104. 1842. TYPE: Country of origin unknown, described from cultivated material (Holotype: not seen and perhaps nonexistent).

    Begonia punctata Link, Kl. & Otto, Ic. Pl. Rar. 1: 17, t. 7, 1840-1844. TYPE: MEXICO: Hort. Berol., December 1842 (Holotype: B!).

    Gireoudia heracleifolia (Schlecht. & Cham.) Kl., Monatsber. Königl. Preuss, Akad. Wiss. Berlin 1854: 125. 1854.

    Gireoudia punctata (Link, Kl. & Otto) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854. 125. 1854.

    Gireoudia heracleifolia var. *viridis* Kl., Abh. Königl. Akad. Wiss. Berlin. 1854: 215. 1855. TYPE: MEXICO: described presum-

ably from material cultivated at Berlin (Holotype: not seen and perhaps nonexistent).

Gireoudia heracleifolia var. *punctata* (Link, Kl. & Otto) Kl., Abh. Königl. Akad. Wiss. Berlin. 1854: 215. 1855.

Begonia heracleifolia var. *nigricans* Hook., Bot. Mag. 83: t. 4983. 1857.

Begonia longipila Lem., Ill. Hortic. 7: 55. 1860, Ill. Hortic. 8: t. 307. 1861. TYPE: MEXICO: described from material sent by Ghiesbreght to Paris (Holotype: not seen and perhaps nonexistent).

Begonia heracleifolia var. *longipila* (Lem.) A.DC., Prodr. 15(1): 335. 1864.

Begonia trigonoptera Sprague, Kew Bull. 218. 1921. TYPE: GUATEMALA: Alta Verapaz: described from caterial collected at Cobá and sent to Kew by Johnson (Holotype: K!) .

Terrestrial, epiphytic or saxicolous occasionally deciduous herbs; *rhizomes* repent, somewhat succulent, 2-18.5 cm long; internodes short, 0.3-1.5 X 0.8-3 cm, densely squamose or squamose-villous when immature with narrow fimbriate-laciniate scales 2-7 (15) mm long or with coarse villi intermixed with narrow barbate basally rounded or flattened trichomes and only occasionally scales. *Leaf blades* simple, straight or rarely oblique, symmetric or occasionally asymmetric, suborbicular or rarely ovate, 4-26 X 3-24 cm, basally broadly shallowly cordate to broadly deeply cordate, apically indistinct or a central lobe more pronounced than other lobes, marginally deeply sinuate-lobed with 5-9 lobes, the lobes commonly 1/3-4/5 the blade length, and often secondarily lobed, primary lobes triangular becoming attenuate-acuminate apically, irregularly incised-dentate to incised-serrate and ciliate-denticulate to ciliate-serrulate and ciliate, glabrous to sparsely glandular or glandular pilose above and beneath with trichomes most dense on principal nerves beneath, 7-10-palmatinerved. *Petioles* 3.5-24.5 (41) cm X 1-8 (11) mm, terete to canaliculate basally or occasionally multicanaliculate throughout, moderately to densely villous, villous-squamose or squamose when immature but only sparsely so at maturity, consisting of very narrow entire to occasionally laciniate scales or a mixture of scales and villi, (2) 5-12 mm long with glandular trichomes commonly intermixed, the indument especially pronounced at the petiole apex with one or more concentric rings of fimbriate-laciniate scales characteristically present. *Stipules* persistent, asymmetrically ovate-triangular, 0.8-1.5 X 0.8-1.2 cm, strongly keeled, apically acute, marginally entire, sparingly pilose throughout or the keel only fimbriate to laciniate. *Inflorescences* generally greatly exceeding the foliage, asymmetric to unilateral, often many-flowered, 3-20 cm diam. *Peduncles* 10.5-66 (86) cm X 1-8 (11) mm, sparsely to moderately villous with both villi and narrow scales frequently intermixed with minute glandular trichomes, but glabrate with age. *Bracts* subpersistent, the lowermost weakly navicular, ovate to narrowly ovate, 0.9-1.7 (2.3) X 0.9-1.7 (2.7) cm, weakly keeled or the keel indistinct, marginally ciliate-serrulate to occasionally glandular-serrulate, but typically margins of secondary bracts glandular-serrulate, sparsely glandular-pilose to glandular externally. *Staminate flowers*: pedicels 3-14 (21) mm long; sepals white to pale or deep pink, transversely elliptic to suborbicular or ovate to ovate-elliptic or oblong, 5.5-15 X (4.5) 5.5-12 mm, glabrous to glandular externally;

petals wanting; stamens 10-32 (35); filaments 0.4-1.8 mm long, inserted on a low torus; anthers narrowly oblong or elliptic to oblong-obovate, 1-2.7 X 0.5-0.9 mm. *Pistillate flowers*: pedicels 4-16 mm long; bracteoles commonly wanting but excrescences or rudimentary bracteoles sometimes present, only rarely bracteolate, bracteoles when present, ovate to elliptic or obovate, (1.7) 3-4.5 (8) X 1.5-2.5 (5.5) mm; sepals colored like staminate sepals, ovate to broadly elliptic, suborbicular or transversely elliptic, 5-12 (15) X 5-12 (14) mm, glandular externally; petals wanting; ovary 7-11 mm long, commonly with a sparse indument of glandular trichomes; styles 3, 1.5-2.5 mm long, connate to 1/2 their length; stigmas lunate to broadly lunate. *Capsules* with pedicels 4-17 mm long, trilocular, 8.5-15 mm long; locule chambers externally appearing ovate to oblong or broadly elliptic, 7-12 X 4.5-8.5 mm; wings 3, unequal or rarely subequal, highly variable in form, the largest asymmetrically ovate to triangular, oblong or often very broadly but shallowly asymmetrically triangular, 6-19 X 8-15 mm, apically acute to subacute or obtuse; the second asymmetric, broadly lunate to shallowly triangular or marginiform, 5.5-10 X 9-15 mm, the third marginiform or very shallowly lunate to lunate-triangular.

DISTRIBUTION AND HABITAT: From the states of Durango and Tamaulipas in Mexico south to Honduras between 50 to 2400 m elevation, with most collections from 50-1600 m. A single specimen, *Cowell 395*, made during an expedition to explore Panama, is the only known collection of this species south of Honduras. Since this area was settled at the time Cowell collected, it is possible that he gathered his material from cultivation. An examination of Cowell's field books in the New York Botanical Garden Library failed to provide any insight into this matter. *Begonia heracleifolia* grows both terrestrially and saxicolously in tropical rain forests and seasonally dry, deciduous forests. In these latter habitats, populations of *B. heracleifolia* may be deciduous (Fig. 19).

FLOWERING: November to April but occasionally flowering during other months.

DISCUSSION: *Begonia heracleifolia* has been widely cultivated since the early nineteenth century in Europe, during which time numerous horticulturally interesting variants were recognized as distinct species or varieties based on one or a combination of characters including leaf blade coloration, depth and extent of leaf lobing and plant size. Both Klotzsch (1855) and Alphonse de Candolle (1864) treated several forms as varieties of *B. heracleifolia*. More recently *B. trigonoptera* was described because of its oblong ovary body and slightly different wing form. These distinctions are minimal compared to the overwhelming similarities between *B. trigonoptera* and *B. heracleifolia*, and do not justify maintaining *B. trigonoptera* as a distinct species. Recognizing the continuous variation existing in many characters of *B. heracleifolia* including coloration, indument, blade lobing depth, inflorescence size and capsule wing form, Smith and Schubert (1961) rightly considered *B. heracleifolia* to be a variable species without any intraspecific taxa.

Despite the previously mentioned differences, *B. heracleifolia* is one of the most readily identified species in sect. *Gireoudia* because of its unusual symmetric or only weakly asymmetric palmately lobed leaves and asymmetric to unilateral cymose inflorescences. Juvenile leaves in seedlings of this species, however, are typically oblique

and asymmetric with a clearly distinguishable apex and shallow lobes at ends of major nerves. In form these leaves are similar to those observed on *B. sericoneura* from southern Central America. *Begonia heracleifolia* appears to begin developing its mature, symmetric, lobed leaves about the time it reaches flowering size, but flowering specimens have been observed with juvenile foliage. Although glandular trichomes have been observed on virtually all species in sect. *Gireoudia*, those of *B. heracleifolia* differ from other species by being borne on longer, more conspicuous stalks and, unlike other species, the persistent or subpersistent inflorescence bracts are typically glandular-serrulate marginally.

In its straight palmately lobed leaves, and lunate stigmas, *B. heracleifolia* is most similar to *B. crassicaulis*, but *B. heracleifolia* can be distinguished from this taxon by its squamose, villous-squamose or villous petiolar indument, its repent rhizomatous habit, its somewhat persistent glandular-serrulate bracts, often ebracteolate flowers and generally strongly unequal capsule wings (Table 9). *Begonia heracleifolia* also resembles other members of the sericoneura species group in its asymmetric, broadly triangular to ovate primary capsule wings. Only two taxa besides *B. heracleifolia* have induments comprised of a mixture of trichome types, *B. cardiocarpa* and *B. strigillosa*. Of these two taxa, only *B. strigillosa* has both villi and scales in its indument, but it differs from *B. heracleifolia* in its oblique to transverse unlobed leaves.

Begonia heracleifolia has been observed in Mexico growing sympatrically with several other species, including *B. nelumbiifolia*. In one region of sympatry, potential hybrids have been encountered. This is discussed in greater detail under *B. nelumbiifolia*.

SPECIMENS EXAMINED: MEXICO. Chiapas: steep moist slope at Yochib, paraje of Kotol Te', Municipio of Tenejapa, 4300 ft, *Breedlove 7372* (DS); slope from Bochil to Simojovel, 4 mi NE of Bochil, Municipio of Bochil, 4500 ft, *Breedlove 8829* (DS, US); rain forest on N shore of Lago Miramar, near San Quintín on Río Jataté, Municipio of Las Margaritas, 1200 ft, *Breedlove 9157* (DS, US); cultivated or growing on sitios of San Cristóbal las Casas, Municipio of San Cristóbal las Casas, 7100 ft, *Breedlove 16043* (DS); limestone ridges, ruins of Yaxchilán on banks of Río Usumacinta, Municipio of Ocosingo, 300 m, *Breedlove 33963* (DS); tropical rain forest, low ridges at confluence of Río Ixcán with Río Lacantum (Río Jataté), Municipio of

TABLE 9. Character differences between *Begonia crassicaulis* and *B. heracleifolia*.

	B. crassicaulis	*B. heracleifolia*
Rhizome orientation	erect to ascending	repent
Adaxial leaf surface	sparsely pilose	glabrous to hirtellous
Petiolar indument	tomentose-lanate	villous, villous-squamose or squamose
Trichome type	fine whiplash trichomes	narrow entire to lacerate scales or mixture of scales and villi
Bracts	marginally ciliate-denticulate to ciliate-serrulate	marginally glandular-serrulate
Bracteoles	pistillate flowers bracteolate	pistillate flowers ebracteolate, only rarely bracteolate
Wings	unequal to subequal	usually unequal, only rarely appearing subequal

Las Margaritas, 300 m, *Breedlove & McClintock 34237* (DS, MEXU); Lacanja, Municipio of Ocosingo, 350 m, *Breedlove 34475* (DS); steep slope with evergreen cloud forest along rd from Toliman to Niquivil, near Ojo de Agua, Municipio of Motozintla de Mendoza, *Breedlove 42605* (DS); 20 mi N of Ocozocoautla along gravel rd to Apitpac near km 31 marker, *Croat 40657* (MO); Hwy 195 between Chiapa de Corzo and Pichucalco, 1080 m, *Croat 46299* (MO); trail between Finca California (at base of S slope of Mt. Ovando and ca 4 km N of Ovando Turquia) and summit of Cerro Ovando, 450-850 m, *Croat 47566* (MO); hillside near Temple of Inscriptions, ruins of Palenque, *Hoover 39* (MO); limestone rocks and ledges at Misola waterfall, *Hoover 42* (MO); camino Piñuela, Escuintla, 300 m, *Matuda 18676* (UC, US); Palenque, *Seler & Seler 5534* (B); paraje of Kulak'tik, Municipio of Tenejapa, 5800 ft, *Shilom Ton 185* (DS); small river in barrio of Tih Ha', paraje of Mahbenchauk, Municipio of Tenejapa, 3600 ft, *Shilom Ton 2012* (DS, DUKE, MEXU, US, WIS); wooded slope near Rancho Viejo of Finca Prusia, Municipio of Angel Albino Corzo, 2400 ft, *Shilom Ton 3608* (DS, US, WIS); near Pantelho, Municipio of Santa Catarina Pantelho, 2800 ft, *Shilom Ton 3665* (DS, WIS); Río Perlas and Río Jataté at San Quintin and near Laguna Miramar, 200 m, *Sohns 1573* (US); tropical rain forest, Palenque Archeological Site, 500 ft, *Thorne & Lathrop 40527* (DS); near Palenque Archeological site, *Utley & Utley 6983* (NOLS); Zandino, near Copainalá, 3800 ft, *Wonderly 37* (MICH). Durango: steep side canyons of Río Tamazula between La Bajada and La Junta, 1300 m, *Breedlove 24505* (CAS, MICH, MO). Guerrero: Distrito Montes de Oca, Vallecitos, *Hinton 11762* (DS, GH, K, MEXU, NY, US). Hidalgo: slopes above Río San Pedro on trail between Calnali and Huazalingo, *Moore 3025* (BH, GH, UC, US); Dist. Huejutla, rd from Huazalingo to Tehuetlán, *Moore 3028* (BH, GH, US); Chapulhuacan, *Moore 4964* (BH). Jalisco: steep rocky mountainsides 8 mi SW of Pihuamo, 500-600 m, *McVaugh & Koelz 1495* (MICH); steep hillside 12-13 km SW of Pihuamo in dense forest, 500-600 m, *McVaugh 24453* (MICH); *McVaugh 26178* (MICH). Michoacan and Guerrero: Río Tecpan, 400 m, *Langlasse 820* (B, GH, P, US). Nayarit: W of Jalcocotan, rocky moist roadside, *Dressler 1044* (GH, MO). Oaxaca: Sta. María Chimalapa, Matías Romero. Col. Cuauhtemoc, Distrito de Juchitán, 225 m, *Delgado, Perino & Garcia 947* (CAS); Chinantla, *Galeotti 195* (BR, P). Trapiche de la Concepción, *Liebmann s.n.* (C); Palomares, Juchitán, *MacDougall s.n.* (NY); District of Tuxtepec, Chiltepec and vicinity, 20 m, *Martínez-Calderón 532* (GH, UC, US); *Martínez-Valderón 566* (UC, US); Distrito Choapam, Yaveo, trail W to Río Yaveo, 435 m, *Mexia 9174* (CAS, GH, MO, NY, UC, US); Río Totulco between Chacalapa and Candelaria on Pochutla-Oaxaca rd, 210 m, *Moore 8275* (BH, US); *8276* (BH); Sierra Madre, *Reiche 572* (M). Sinaloa: 19.1 mi E of Río Concordia at Concordia on Mexico 40, Municipio de Rosario, 2900 ft, *Breedlove 1623* (DUKE, MICH); Hwy 40, 29.9 mi E of Concordia, 4800 ft, *Breedlove 4247* (DUKE); N facing damp bank on rd from Mazatlan to Durango, near La Guayanera, 1000-1500 m, *Hoover s.n.* (GH). Tabasco: base of Cerro de Madrugal, ca 4 km SE of Teapa on rd to Tacotalpa, 300 m, *Croat 47903* (MO). Tamaulipas: Cañon de Gómez Farias, *Duke 3586* (MO); *Martin 12* (MICH); *Palmer 351* (US); without locality, *Palmer 283* (US). Veracruz: Zongolica, 1252 m, *Alvarado 1* (US); Orizaba, *Botteri 328* (GH, US); *Botteri & Sumichrast 1595* (P, US); *Botteri & Sumichrast 1670* (P); Córdova, *Bourgeau 1583* (BR, C, F, GH, K, MEXU, NY, P, US); *Bourgeau 1983* (GH, P, US); Laguna Encantada 7 km al NE of San Andres Tuxtla, *Cedillo & Calzada 83* (MEXU, MO); Hidalgotitlan, 130-150 m, *Dorantes et al. 2815* (MEXU, MO); Wartenberg, near Tantoyuca, *Ervendberg 268* (GH); Orizaba, *Gray s.n.* (GH, USF); Córdoba, *Greenman 137* (GH); Santiago Tuxtla, *Kelly 925* (UC); Fortin, *Kerber 205a* (CAS, UC); km 324, carreterra a Fortin, *Langman 3417* (MEXU, US); N of Fortin, *Langman 4124* (US); Colipa, *Liebmann s.n.* (C); Mirador, *Liebmann s.n.* (C); *Linden 34* (K); Atoyac, *Martinez 208* (US); Suchilapa, *Mell 529* (NY, US); Orizaba, *Muller s.n.* (NY); Catemaco, *Nelson 432* (US); Sanboru, *Orcutt 3076* (CAS, DS, MO); bluffs of Barranca of Chavarrillo, near Jalapa, 3500 ft, *Pringle 7797* (US, VT); Zacuapan and vicinity, *Purpus 2421* (UC, US); *Purpus 4376* (UC); *Purpus 5757* (UC); *Purpus 6350* (UC); *Purpus 7130* (UC); Orizaba, *Rosas 259* (CAS, MEXU); San Miguel, Orizaba, *Schubert & Rojas 1836* (US); near river, Atoyak, just outside Córdoba, *Schubert & Rojas 1840* (US); Santa Lucrecia, isthmus of Tehuantepec, *Smith 1007* (GH, MEXU, MO, NY, UC, US); Fortin, *Troll 51* (M); Brecha Hnos. Cedillo-Agustin Melgar, Hidalgotitlan, *Vasquez et al. 49* (C); *Vasquez et al. 495* (BM, MEXU, MO); El Puente, Municipio de Teocelo, 1000 m, *Ventura 7834* (MICH); Río Tonto. Ejido de Almilinga, 6 km W of Campo Experimental de Hule, El Hulmar, Zongolica, *Vera Santos 2822* (MICH). Fortuño, Coatzacoalcos River, 30-50 m, *Williams 8603* (MICH). Yucatán and Tabasco: *Johnson 131* (K). Without locality, *Kerber 502* (US). BELIZE. Toledo: Maya Mountains between forestry camp and San José, *Boutin & Schlosser 5194* (BM, MO); rocks in high ridge, Sulphur Hill, Edwards road beyond Columbia, *Gentle 6367* (F, LL); *Gentle 6416* (LL). Without district: river bank of Río Grande, *Schipp 8-449* (F); Pueblo Viejo, 1700 ft, *Schipp S-695* (BM, F, GH, MICH, MO, NY). GUATEMALA. Alta Verapaz: Sebol,

high forest about 4 km on Cobán Rd., *Contreras 4347* (LL); near Finca Sepacuite, *Cook & Griggs 654* (US); Pancajché, *Muenscher 12564* (BH); *Standley 70777* (F); *Standley 70808* (F); Río Polochic, near Pancajché, 360 m, *Standley 92010* (F); vicinity of caves, SW of Lanquín, 600-1000 m, *Steyermark 44122* (F, GH, US); stone wall of municipal building Cobán, 1320 m, *Williams et al. 40656* (F). Chimaltenango: lower and middle SW slopes of Volcán Fuego, along Barranco Espinzao and tributary of Río Pantaleon, 1200-1600 m, *Steyermark 52115* (F). Chiquimula: Volcán Ipala, near Amatillo, 900-1510 m, *Steyermark 30471* (F); Río Tacó, between Chiquimula and Montaña Barriol, 3-15 mi NE of Chiquimula, 500-1200 m, *Steyermark 30623* (F). El Progresso: trail between Finca Pianonte E to San Miguel, passing Finca Polonia, Finca Delicias aldea Cimiento, *Steyermark 43747a* (F). Guatemala: without further locality, 5000 ft, *Donnell Smith 1859* (GH, K, US); about 4 mi N of Guatemala City, road to Chinautla, 4400 ft, *White 5189* (MICH). Huehuetenango: between Ixcán and Río Ixcán, Sierra de los Cuchumatanes 150-200 m, *Steyermark 49212* (F); Paso del Boquerón, Río Trapichillo below La Libertad, 1200-1300 m, *Steyermark 51174* (F). Izabal: Los Amates, 160 ft, *Deam 19* (GH, MICH). Jalapa: mountains about Chahuite, NW of Jalapa, 1650 m, *Standley 77514* (F). Petén: Poptún-San Luis road, in high rain forest of SE Peten, *Lundell 16464* (LL); Río Pasion Basín, Río Pucte, ENE of El Pucte camp, on trail to La Libertad, *Lundell 18206* (LL); forest between Finca Yalpemech along Río San Diego and San Diego on Río Cancuen, 50-100 m, *Steyermark 45420* (F, GH, NY); camino para Santa Ana, a km 15, lado NE, *Tún Ortíz 1669* (BM, F, NY, US). Zacapá: Rillito del Volcán de Monos, Volcán de Monos, 1150-2150 m, *Steyermark 42344* (F, GH); valley of Vegona, between Vegas and Calera, 1200 m, *Steyermark 42977* (F, GH, US). HONDURAS. Comayagua: Siguatepéque, 1050-1400 m, *Standley 56514* (F, US). Morazán: region of Chahuité, 800-1075 m, *Standley, Molina & Chacon 5020* (F). Ocotepeque: terrestrial on slope of river Yoronte between El Moral and Sinuapa, 1300 m, *Molina 24194* (F); Agua Caliente river banks, Honduras-Guatemala border, 900 m, *Molina, Molina & Molina s.n.* (MO). EL SALVADOR. Without further locality, *Calderón 2311* (US). PANAMA: Canal Zone: Corozal to Pedro Miguel, *Cowell 395* (NY). Source unknown: Hort. Berol. (HAL).

19. *Begonia crassicaulis* Lindl., Bot. Reg. 28: misc. 22, t. 44. 1842.
TYPE: GUATEMALA: without further locality. *Hartweg s.n.* (Holotype: CGE!)

Gireoudia crassicaulis (Lindl.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

Terrestrial or epiphytic, often deciduous herbs; *rhizomes* erect or ascending, often branched, succulent, 5-30 cm high; internodes short, 0.8-2.5 X 1-3 cm, densely villous when immature with whiplash trichomes intermixed with narrow barbate, basally rounded or flattened trichomes 2-5 mm long. *Leaf blades* simple, membranaceous to chartaceous, straight, symmetric, suborbicular to transversely broadly oblong-elliptic, 12-17 X 19.5-23 cm, basally shallowly cordate to broadly, deeply cordate, apically poorly defined without a distinct apex, or rarely attenuate-acuminate, marginally deeply palmately 6-8-lobed and often secondarily lobed, lobes straight to subfalcate, lanceolate to narrowly triangular becoming attenuate-acuminate apically, irregularly incised-dentate to incised-serrate and ciliate-denticulate to ciliate-serrulate and ciliate, sparsely pilose throughout above and in intercostal regions beneath but moderately or densely tomentose on principal nerves, palmately 6-8-nerved. *Petioles* 11.3-28 cm X 4-11 mm, moderately to densely tomentose-lanate when immature, but only sparingly so with age, with antrorsely spreading whiplash trichomes 0.5-6 mm long, often with glandular trichomes intermixed. *Stipules* subpersistent, asymmetrically ovate, 12-17 X 9-13 mm, weakly keeled, apically acute, marginally entire, glabrous or glandular throughout. *Inflorescences* strongly asymmetric to unilateral, laxly to densely cymose, few- to many-flowered, 6.5-25 cm diam. *Peduncles* 7.8-18.5 (53.6) cm X 1-5 (10) mm, glabrate to densely tomentose-lanate. *Bracts* caducous, the lowermost somewhat navicular, very broadly obovate, 9-13 X 8-11 mm, apically obtuse, marginal-

ly ciliate-denticulate to ciliate-serrulate; glabrous to sparsely pilose and often glandular. *Staminate flowers*: pedicels 0.7-1.3 (2) cm long; sepals suborbicular to broadly obovate, 6-14 X 5.5-13 mm, glabrous; petals wanting; stamens 14-26; filaments 0.5-1.3 mm long, inserted on a slightly raised torus; anthers oblong to narrowly obovate, 0.8-2.1 X 0.5-1 mm. *Pistillate flowers*: pedicels 1.3-2 cm long; bracteoles subpersistent, obovate to suborbicular, 5.5-10 X 6-9 mm, apically rounded, marginally irregularly serrulate-denticulate, glabrous; sepals broadly obovate to suborbicular, 5-15 X 5-14 mm; petals wanting; ovary 1-1.5 cm long, glabrous throughout; styles 3, 2-2.5 mm long, connate 1/4-3/4 their length; stigmas broadly lunate. *Capsules* with pedicels 1.5-2.4 cm long, trilocular, 1.3-1.7 cm long; locule chambers externally appearing suborbicular to broadly elliptic or obovate, 1-1.3 X 0.6-0.9 cm; wings 3, unequal to somewhat subequal, the largest asymmetrically lunate to broadly triangular, 7-12 X 10-16 mm, apically obtuse, the second asymmetrically triangular, 9-11 X 7-16 mm, the third marginiform or similar to the second.

DISTRIBUTION AND HABITAT: *Begonia crassicaulis* is reported from Guatemala and most recently Mexico (*Moore, s.n.*, US) at elevations between 1100-1400 m where it is found in exposed locations, often growing epiphytically (Fig. 8).

FLOWERING: January-March and possibly into May.

DISCUSSION: *Begonia crassicaulis* is one of the more poorly known species in sect. *Gireoudia* occurring in Central America, represented by only a handful of collections. Compounding problems inherent in studying little material is the absence of leaves from most herbarium specimens because *B. crassicaulis* characteristically flowers when leafless. In addition to being deciduous, *B. crassicaulis* typically has thick, succulent rhizomes and it is likely that these characters enable *B. crassicaulis* to succeed in seasonally very dry habitats or in sunny, exposed locations.

Sterile specimens of *B. crassicaulis* may be readily confused with *B. heracleifolia* since both taxa have symmetric, palmately lobed leaves. These taxa, however, differ in their rhizome orientation which is erect or ascending in *B. crassicaulis* but repent in *B. heracleifolia* and in their petiolar indument. *Begonia crassicaulis* is one of few species with a tomentoselanate indument of fine whiplash trichomes, while the indument of *B. heracleifolia* is squamose, villous-squamose or villous resulting from various mixtures of broad lacerate scales and coarse villi. Both *B. crassicaulis* and *B. heracleifolia* have strongly asymmetric to unilateral inflorescences, but bracts are commonly persistent to subpersistent on inflorescences of *B. heracleifolia* while they are caducous on inflorescences of *B. crassicaulis*, so that they can readily be distinguished. Bracts also differ in margination between these species, with those of *B. crassicaulis* being ciliate-denticulate to ciliate-serrulate while those of *B. heracleifolia* are typically glandular-serrulate (Table 9).

Begonia crassicaulis forms a part of the sericoneura species group. All taxa in this group are characterized by indu-ments of whiplash trichomes, bracteolate pistillate flowers, lunate stigmas and primary capsule wings that are asymmetrically lunate to lunate-triangular, triangular or ovate. Within this group, *B. crassicaulis* is most similar morphologically to *B. sericoneura*. Both species have generally thick, succulent, erect to ascending rhizomes. Although *B. sericoneura* frequently loses most of its leaves during the dry season, leaves are

always present on flowering plants, while in *B. crassicaulis* flowering apparently commences while the rhizomes are leafless. These taxa differ in several significant characters including leaf orientation, lobing, stamen number and capsule wings. The straight palmately sinuate-lobed leaves of *B. crassicaulis* are a marked contrast to the oblique to transverse, dentate or serrate to doubly dentate-serrate or irregularly lobed leaves of *B. sericoneura*. Staminate flowers of *B. crassicaulis* generally bear fewer stamens than those of *B. sericoneura*. Capsule wing size will also distinguish these species. In *B. crassicaulis*, the largest capsule wing is typically more shallow than that observed in *B. sericoneura*, but its remaining wings are larger than those of *B. sericoneura* (Table 10).

SPECIMENS EXAMINED: MEXICO. Guerrero: cultivated material from steep banks along small river to Cañada de Colotlipa between Chilpancingo and Colotlipa, *Moore s.n.* (US).

TABLE 10. Morphological comparison of *Begonia conchifolia, B. crassicaulis, B. plebeja* and *B. sericoneura*.

	B. conchifolia	*B. crassicaulis*	*B. plebeja*	*B. sericoneura*
Rhizome habit	repent	upright to semi-upright	repent	upright to semi-upright
Rhizome diameter (cm)	(0.15)0.25-0.6(1.1)	1-3	0.8-1.8(2.5)	0.8-1.8
Leaves	persistent	deciduous	often deciduous	often semi-deciduous
Veination	peltinerved	palminerved	palminerved	palminerved
Blade orientation	oblique	straight	oblique to transverse	oblique to transverse
Blade size (cm)	2-9(14) X 1-8(10)	12-17 X 19.5-23	6-18(23) X 4-13(18)	(4)7-14(22) X (4)6-12(16)
Margination	denticulate-serrulate	deeply palmately lobed	dentate-cuspidate or doubly dentate	dentate or serrate to doubly dentate, occasionally irregularly lobed
Petiolar indument	moderately to densely tomentose-lanate	densely tomentose-lanate when immature	sparingly to moderately pilose	densely lanate when immature
Trichome base	uniseriate	multiseriate	multiseriate	multiseriate
Staminate sepal size (mm)	4-8(13) X 4-8(10.5)	6-14 X 5.5-13	3.5-6.5 X 2.8-6.5	(6)8-14 X 8-14(16)
Stamens	6-13	14-26	11-21(24)	(14)28-61
Stigmas	lunate	lunate	lunate	broadly lunate
Capsule length (cm)	0.4-1	1.3-1.7	(0.9)1.1-1.5	0.9-1.6(1.8)
Capsule wings	subequal	unequal to subequal	unequal	unequal
Dorsal wing	asymmetrically lunate to lunate-triangular	asymmetrically lunate to broadly triangular	asymmetrically triangular to ovate	broadly triangular to ovate

GUATEMALA. Chimaltenango: lower and middle SW slopes of Volcán Fuego, above Finca Montevideo, 1200-1600 m, *Steyermark 52115* (F, GH). Quetzaltenango: San José. B.V. Costa Cuca, *Rodriguez 240* (P); *Rodriguez 241* (P); *Rodriguez 455* (P); between Finca Pirineos and Finca Soledad, lower S facing slopes of Volcán Sta. María, between Sta. María de Jesús and Calahuaché, 1300-1400 m, *Steyermark 33558* (F, US). Sacatepéquez: dry secondary forest, lower slopes of Volcán Fuego, 7 km SW of Alotenango, 1100 m, *Williams & Williams 43513* (F, MICH).

20. *Begonia sericoneura* Liebm., Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1852: 13. 1852. TYPE: NICARAGUA: In monte Pantasmo, in prov. Segovia, January, *Oersted s.n.* (Holotype: C!; isotype: B!).

Gireoudia fibrillosa Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854. *nom. nud.*

Gireoudia pilifera Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854. *nom. nud.*

Gireoudia sericoneura (Liebm.) Kl., Abh. Königl. Akad. Wiss. Berlin 1854: 209. 1855.

Gireoudia fibrillosa Kl., Abh. Königl. Akad. Wiss. Berlin 1854. 206. 1855. TYPE: CENTRAL AMERICA: Chiriquí: described from cultivated material sent to Mathieu at Berlin by Warscewicz (Holotype: B!).

Gireoudia pilifera Kl., Abh. Königl. Akad. Wiss. Berlin 1854: 206. 1855. TYPE: CENTRAL AMERICA: Chiriquí, described from cultivated material sent to Mathieu at Berlin by Warscewicz under #1708 (Lectotype: B!; isolectotype: B!)

Begonia pilifera (Kl.) A.DC., Prodr. 15(1): 337. 1864.

Begonia biolleyi C.DC., Bull. Soc. Bot. Belg. 35(1): 263. 1896. TYPE: COSTA RICA: Bord du Río Ceibo près Buenos Aires, janvier. *Pittier 6567* (Lectotype: G!; isolectotype: BR!).

Begonia nicaraguensis Standl., Field Mus. Nat. Hist. Bot. Ser. 4: 237. 1929. TYPE: NICARAGUA: On rocky cliffs and boulders in shade near Miranda Bodega, at the confluence of Tunkey and Murcielago creeks, region of Bragmann's Bluff, 25 m, *Englesing 149A* (Holotype: F!).

Begonia hypolipara Sandwith, Kew Bulletin 1931: 99. TYPE: HONDURAS: San Pedro, described from cultivated material taken to Kew by Cott (Holotype: K!).

Begonia lindleyana sensu Smith & Schubert, *pro parte major,* Caldasia 4: 11. 1946. *et seqq.*

Acaulescent or caulescent herbs; *rhizomes* fleshy, green but silver-gray with age, often procumbent when young but with age upright to semi-upright, with further elongation becoming declined and eventually decumbent, then rooting and re-establishing an erect posture, 0.4-10 dm long; internodes short to elongate, 0.3-2.8 X 0.8-1.8 cm, strongly lenticellate, moderately to densely villous with whiplash trichomes and coarse barbate basally rounded trichomes intermixed. *Leaf blades* simple, chartaceous to membranaceous, oblique to transverse, asymmetrically ovate, suborbicular or broadly elliptic, (4) 7-22 X (4) 6-16 cm, basally shallowly to deeply cordate, apically acute to attenuate-acuminate, infrequently obtuse or ill-defined, marginally variable, ciliate and ciliate-denticulate to ciliate-serrulate, frequently dentate, doubly dentate to doubly serrate or acutely to acuminately lobed at ends of major

nerves, hirsute to sparingly pilose throughout above and densely lanate beneath when unexpanded, becoming sparingly pilose or sericeous in intercostal regions and sparingly to densely lanate on principal nerves, palmately (5) 6-7 (9)-nerved. *Petioles* light green but often suffused with red distally, 4-22 (26) cm X 1.5-4 (7) mm, densely lanate when immature becoming sparsely to moderately so or sericeous with age, the whiplash trichomes 1.5-5 mm long. *Stipules* persistent, scarious with prominent fuscous-ferrugineous nerves and hyaline intercostal regions that characteristically disintegrate with age, asymmetrically triangular, ovate or broadly lanceolate, 1.3-2.2 X 0.7-1.1 cm, weakly to strongly keeled, apically attenuate-acuminate, marginally entire, glabrous to sparingly pilose throughout or the keel only pilose. *Inflorescences* typically greatly exceeding the foliage, slightly to moderately asymmetric or unilateral, densely cymose, many-flowered, 6-26 cm diam. *Peduncles* light green, often deeply suffused with red, (12) 15-55 cm X 2-8 mm, moderately lanate when young, becoming sparingly to densely pilose with age. *Bracts* deciduous to caducous, light green, frequently suffused pink, the lower 2 equitant in bud, unequal, obovate to obtriangular, 1.7-2.2 X 1.5-2.5 cm, apically obtuse, marginally ciliate and ciliate-denticulate to ciliate-serrulate. *Staminate flowers*: pedicels 8-22 mm long; sepals white to pink, suborbicular to broadly elliptic or ovate, (6) 8-14 X 8-14 (16) mm, glabrous or occasionally sparingly pilose externally; petals wanting, stamens (14) 28-61; filaments (0.3) 0.5-1.5 (2) mm long, inserted on a low torus; anthers oblong to narrowly obovate or elliptic, 1-1.5 (2) mm long. *Pistillate flowers*: pedicels 5-18 mm long; bracteoles deciduous, light green or white, frequently suffused with pink, submembranaceous, unequal, the larger transversely elliptic, very broadly obovate or occasionally subrhomboid, (4) 6.5-9 X (8) 9-13 mm, the smaller suborbicular to obovate, 4.5-7 X 5-8 mm, both apically obtuse, marginally ciliate-denticulate and ciliate, sparingly pilose throughout; sepals colored like staminate sepals, suborbicular to transversely elliptic, 5-10 X 7-15 mm, externally glabrous or sparingly pilose; petals generally wanting, but when present, 1, white, rudimentary or obovate, oblanceolate, 3 X 1 mm; ovary (4) 7-10 mm long, glabrous; styles 3, 1-3 mm long, connate briefly to 1/3 their length; stigmas broadly lunate with ends beginning to spiral. *Capsules* with pedicels 10-28 mm long, trilocular, 9-16 (18) mm long; locule chambers appearing broadly elliptic, oblong or obovate, 7-11.5 (14) X 6-9.5 (11.5) mm; wings 3, unequal, the largest asymmetric, often somewhat subfalcate, broadly triangular to ovate, (9) 10-16 (18) X 10-16 (20) mm, apically oblique, acute to obtuse, rarely truncate, the second asymmetric, lunate to very broadly triangular, 5-9 X (8) 9-16 (18) mm, the third marginiform.

DISTRIBUTION AND HABITAT: Northeastern Oaxaca in Mexico, through Central America to Colombia from sea level to 1200 m. *Begonia sericoneura* inhabits wet tropical and lower montane areas where it grows as a low epiphyte, terrestrially in open or disturbed areas along roadsides and on exposed rocks, as well as in dense, virgin forests. Its fleshy, silver-gray rhizomes, leaves with thick hypodermi, and deciduous or semi-deciduous habit are likely important in enabling this taxon to successfully colonize drier microhabits of potentially high insolation where it is often encountered. (Fig. 18).

FLOWERING: December-April.

DISCUSSION: *Begonia sericoneura* is one of the most commonly collected

species in Central America and is readily distinguished from other taxa by its fleshy, ascending rhizomes with persistent stipules, pilose to lanate petioles, semipersistent secondary bracts and bracteolate pistillate flowers. Despite its relatively constant rhizome, stipule, indument and floral characters, *B. sericoneura* exhibits significant variation in leaf margination over its range and within more limited geographic areas. Specimens from Mexico, Belize and Guatemala possess leaves that are apically obtuse to acute with margins that are ciliate and denticulate, but typically only weakly dentate. In contrast, specimens from Nicaragua, Costa Rica and Panama are apically acuminate to attenuate-acuminate and marginally most often strongly lobed and dentate. Because *B. sericoneura* is widely distributed and variable in leaf margination, it is not surprising that it has been described several times from different geographic areas. The most recent, *B. hypolipara* from Honduras has leaves characteristic of *B. sericoneura* from northern Central America and should not be maintained as a distinct species, nor does it warrant infraspecific recognition.

Begonia sericoneura formed the major element in *Begonia lindleyana* sensu Smith and Schubert (1946b, 1961), a species from which it can be distinguished by vegetative morphology alone. In both its bushy habit and peltate leaves, characters Ziesenhenne (1972) recognized as important in delimiting *B. lindleyana, B. lindleyana* stands apart from *B. sericoneura*. Floral characters also conclusively establish that *B. sericoneura* is distinct from *B. lindleyana* and, furthermore, are evidence that *B. lindleyana* may be incorrectly placed in sect. *Gireoudia*. (This is discussed under doubtful and excluded species in greater detail.) The bracteolate pistillate flowers with three stigmas found in *B. sericoneura* are markedly different from the ebracteolate pistillate flowers with four stigmas observed in *B. lindleyana*. With two notable exceptions, *B. cardiocarpa* and *B. sarcophylla* which are discussed elsewhere, the remaining taxa Smith and Schubert (1946b, 1961) treated as *B. lindleyana* belong in *B. sericoneura*. However, Doorenbos (1980) relying on cultivated material and horticultural literature, but with no apparent recourse to critical herbarium specimens including types, considered *B. lindleyana* very variable and concurred with Smith and Schubert's initial treatment of this species (Smith and Schubert, 1946b). It is likely that *Gireoudia fibrillosa* represents a depauperate form of *B. sericoneura*, and herein is considered conspecific with *B. sericoneura*. In leaf blades, stipules, pubescence, bracteole and stigma characters, this taxon is very similar to collections of *B. sericoneura* from Costa Rica. The stamen number, 14-16, is however lower than that counted in any other staminate flower from Costa Rica or elsewhere in Central America (28-61). The primary wing on the ovary in the specimen of *G. fibrillosa* is also less asymmetrically triangular than those observed in most pistillate flowers of *B. sericoneura*. *Begonia pilifera* is indistinguishable from *B. sericoneura* and was treated as a synonym of *B. lindleyana* sensu Smith and Schubert along with *B. biolleyi* (Smith and Schubert, 1946b, 1961). One of the two specimens of *Warscewicz 1708* at Berlin was selected as the lectotype of *G. pilfera*. A lectotype was also selected for *B. biolleyi, Pittier 6567* at Geneva, from the several collections cited by Casmir de Candolle.

Begonia sericoneura (as *B. lindleyana* sensu Smith and Schubert) has been frequently confused with *Begonia plebeja* because cyme characters utilized to dis-

tinguish the taxa (Smith and Schubert, 1961) prove inconstant. Although cymes of *B. sericoneura* are often only slightly to moderately asymmetric, numerous individuals produce strongly asymmetric to unilateral inflorescences, while the converse is true in *B. plebeja*. These species can be separated unequivocally by most other vegetative and floral characters, including rhizome form, stipules, pubescence patterns, stamen number, bracts and stigma form.

Begonia sericoneura is most closely allied to *Begonia crassicaulis* and, despite similarities in certain vegetative and floral characters, there are major differences between these taxa. Although leaves of *B. sericoneura* are variable, they never approach the symmetric, palmately nerved and lobed leaves characteristic of *B. crassicaulis*. When leaves of *B. crassicaulis* are wanting, these species may be separated by stamen number and wing characters. The primary wing on capsules of *B. sericoneura* is typically larger than that observed on *B. crassicaulis* while the remaining wings are generally more shallow on *B. sericoneura* than on *B. crassicaulis*. The relationship between these species is discussed in greater detail under *B. crassicaulis*. *Begonia sericoneura* is also allied with *B. conchifolia* and *B. plebeja* which share similar induments of whiplash trichomes, bracteolate pistillate flowers and similar primary capsule wing form. The distinctions between these taxa are presented in discussions of *B. conchifolia* and *B. plebeja* and in Table 9.

Because of its relatively broad geographic and elevational distribution, *B. sericoneura* is sympatric with a large number of other species in sect. *Gireoudia*. Individuals are frequently found growing intermixed with, or in close proximity to one or more species in the section, including *B. cardiocarpa, B. conchifolia, B. corredorana, B. crassicaulis, B. manicata, B. multinervia* and *B. urophylla*. When *B. sericoneura* is sympatric with other species, hybrids often form. The evidence for this is presented with *B. conchifolia, B. corredorana* and *B. urophylla*.

SPECIMENS EXAMINED. MEXICO. Chiapas: tropical rain forest on W side of Laguna Miramar E of San Quintín, Municipio of Las Margaritas, 350 m, *Breedlove 33141* (DS, MO); Temple walls of ruins of Bonampak, *Hoover 44* (MO, NY); small river in barrio of Tih Hi', paraje of Mahbenchauk, Municipio of Tenejapa, *Shilom Ton 1455* (DS, US). Oaxaca: Tehuantepec, *Orcutt 3359* (MO); tropical forest, Cerro Aruarillo, Finca San Cristóbal, near Valle Nacional, 150 m, *Schultes & Reko 600* (GH). Quintana Roo: ruins at Coba, *Lundell & Lundell 7691* (MEXU, MICH). BELIZE. Belize: Gracie Rock, 1.5 mi S of Mile 22 on Western Hwy, *Croat 23857* (DUKE, MO); *Gentle 1537* (F, GH, MICH, MO, NY, US); *Liesner & Dwyer 1463* (MO). El Cayo: river bluffs, El Cayo, *Bartlett 11501* (F, MICH); *Bartlett 13006* (F, MICH, US); on rocks near Camp 6, *Gentle 2364* (F, GH, MICH, NY, VT); line W of Hummingbird Hwy, N boundary of Roaring River Est., 90 m, *Spellman & Newey 1985* (MO). Toledo: in Condemn Branch hills, *Gentle 5140* (F, LL, MICH, US); on rock in acahual, hill slope, Cero, *Gentle 6969* (LL, US); rocky wooded hills, *Peck 817* (GH, NY); S peak of Saddle Back, approx. 2.5 mi NW of Punta Gorda, 300-500 ft, *Proctor 35823* (F, GH, MICH, MO, NY); Aguacarte, *Whiteford 1618* (BM). District unknown: Jacinto Hills, 400 ft, *Schipp 1300* (BM, F, GH, MICH, MO, NY); caves, without further locality, 100 ft, *Schipp 8-182* (BM, F, MICH, MO, NY); Caves Branch, Mountain Cow, *Whiteford 1204* (BM). GUATEMALA: Alta Verapaz: trail to Panzas, Semacoch, *Goll 252* (US); *Goll 253* (US); vicinity of caves SW of Lanquín, 600-1000 m, *Steyermark 44095* (F, GH); Río Icvolay N and NW of Finca Cubilguitz to Quebrada Diablo, 300-350 m, *Steyermark 44724* (F, GH); Finca Transvaal, 2000 ft, *Wilson 297* (F). Huehuetenango: cafetal of Finca Soledad, 5 mi SE of Barillas, Sierra de los Cuchumatanes, 1150 m, *Steyermark 49546* (F, GH). Izabal: mixed rain forest on calcareous slopes 13 km E of jct of CA9 and rd to San Filipe, 60 m, *Harmon & Fuentes 1898* (F, MO). Petén: La Libertad and vicinity, *Aguilar 418* (F, MICH); Maya ruins, Tikal, *Bartlett 12582* (F, GH, MICH, NY, US); *Lundell 15333* (Duke, LL, MICH, US); *Tún Ortíz 727* (F, MO, NY, US); *Tún Ortíz 1684* (BM, DUKE, F); foresta alta, en orillando el camino para Puerto Mendez, 164

km de Santa Elena, *Tún Ortíz 767* (F, LL); Río Santa Isabel, between mouth of Río Sebol and El Porvenir, 100 m, *Steyermark 45842* (F, GH). Verapaz and Chiquimula: eastern portions, without further locality, *Watson 203* (GH, US). HONDURAS. Atlantida: paderones y rocas de Río Pajuil, entre El Progresso y Tela, 200 m, *Molina 10499* (F, NY); Lancetilla Valley near Tela, 200-600 m, *Standley 56901* (F, US); *Yuncker 5082* (F, MICH, MO); thick forest along trail on slopes of Mt. Cangrejal, back of La Ceiba, *Yuncker, Koeper & Wagner 8469* (BM, F, GH, MICH, MO, NY, US). Colón: Río Negro Dam, 1.5 mi SE Trujillo, *Saunders 202* (BM). Comayagua: dense tropical forest, Siguatepéque, 3200 ft, *Edwards 729* (F, GH, NY); Taulabé, Quebrada La Caliche, *Garcia 32* (MO); *Yong 273* (MO). Cortés: Montaña La Cumbre, Cordillera de Omoa al NW de San Pedro Sula, 200 m, *Molina 6725* (F, LL). El Paraíso: trail, Danlí to Finca La Emilia, *Carlson 2547* (in part) (F); *Carlson 2549* (F, MICH); *Molina 5092* (F); Río Guayambre, Valle Jamastran, 350 m, *Molina 7352* (F); paderones humedos cerca del Mineral de Aqua Fria, 1400 m, *Molina 7650* (F, US); Matorrales entre El Nance y Valle Jamastran NW of Chichicaste, 400 m, *Molina 8796* (F); wet rocky thicket, Quebrada del Ingenio de Los Angeles near Yuscarán, 900 m, *Standley et al. 1736* (F); *Williams & Molina 11189* (F). Morazán: paderones de Quebrada del Zorillo al SW de Talanga, 110 m, *Molina 7811* (F, US); Zamorano, 800 m, *Rodriguez 3586* (F, GH); San Antonio de Occidente, 850 m, *Rodriguez 3659* (F, GH); El Zamorano, 780-900 m, *Standley 5137* (F); *Standley 5186* (F). Olancho: dentro del matorral de Quebrada Catacamas en Montaña Peña Blanca, 900 m, *Molina 8392* (F, NY); Río Wampú en selvas humedas de maderas duras, cuesta de camino 15 km N de Pisijire, *Nelson & Clewell 540* (MO, NY); 500-700 m, *Nelson & Clewell 717* (F); moist quebrada between Juticalpa and El Asilo, 380-400 m, *Standley 17753a* (F); Juticalpa, 380-400 m, *Standley 17873* (F); trail between Catacamas and La Prensa, N of Catacamas, 500-600 m, *Standley 18259* (F). Santa Bárbara: rocky beaches on island in Lake Yojoa, near Research Camp, 2200 ft, *Allen 6466* (DS, F); disturbed slope along gravel rd on NW side of Lago de Yojoa, 700 m, *Croat 42753* (MO); San Pedro Sula, 1000 pp, *Thieme 5238* (GH, K, US). Yoro: foothills near Medina, Aguan River Valley, Coyoles, 625 ft, *Yuncker, Koepper & Wagner 8642* (BM, F, GH, MO, NY, US). NICARAGUA: Bluefields: primary rain forest 5 km NE of Rama, Rama and vicinity of Río Escondido, *Proctor, Jones & Facey 27314* (F, LL, MICH, NY). Chontales: *Seemann 46* (BM, K). Jinotega: disturbed cloud forest Hwy 3 from Jinotega to Matagalpa, 5-8 km SW of Jinotega, *Croat 43086* (MO); sierra W of Jinotega, trail to Cerro de la Cruz, 1050-1350 m, *Standley 10183* (F); *Standley 10289* (F); cut-over area along Tuma Lake N of Jinotega, 1000 m, *Williams et al. 27395* (F). Matagalpa: between Matagalpa and El Tuma, 3000 ft, *Bunting & Licht 1016* (F, NY, US); Yasica forest, 26 km S of Matagalpa on road to El Tuma, 400 m, *Molina 20505* (F, NY); premontane wet forest, Salto Grande of Quebrada Negra and valley of Río Bilampi, W and NW of Cerro Musun, 500-800 m, *Neill 1758* (MO); slopes at Río Tuma bridge on Hwy 5, ca 33.2 km from Hwy 3 intersection, 340 m, *Stevens 6026* (BM, MO); cloud forest area, Sta. María de Ostuma, Cordillera Central between Matagalpa and Jinotega, 1300-1500 m, *Williams, Molina & Williams 24674* (F, NY); cut over hills about 15 km NE of Matagalpa along Río Las Cañas, 700-800 m, *Williams et al. 27523* (F, NY, US). Nueva Segovia: gallery forest and riverine vegetation along Río Solonli (or Río Arriba Jalapa) 5 km N of Jalapa, 700-900 m, *Neill 1635* (MO); Sangsangta, *Schramm 28* (US); steep granite slopes of narrow quebrada to Cerro El Peñascal, 1125 m, *Stevens 3274* (MO). Rivas: N slope of Volcán Maderas, Isla Ometepec in Lago Nicaragua, 600 m, *Neill & Vincelli 3204* (MO); Stevens *6570* (MO). Zelaya: forest N and NE of La Luz, vicinity of La Luz-Siuna, 150-200 m, *Bunting & Licht 543* (F, GH, US); area del Ocotal, Río Grande, *Molina 2337* (F); rain forest near Siuna, Mt. Liveco, Madregava, *Narvaez 3060* (US); *Narvaez 3061* (MO); Río Yaoya, 4 km S of crossing of Siuna-Rosita hwy, 100 m, *Neill 3809* (MO); unnamed cerro 3 km S of Cerro Bacan, 240-260 m, *Neill 3912* (BM, MO); near Siuna, 250-500 m, *Seymour 3206* (MO); upriver from bridge over Caño Sardina along rd to Colonia Yolaina and Colonia La Esperanza, 180-200 m, *Stevens 6305* (MO); S slope of Cerro El Inocente, near Caño Majagua, 800-1000 m, *Stevens* 6777 (MO); trail from Cerro Saslaya to San José Hormiguero, between Caño Majagua and Caño Sucio, 600-800 m, *Stevens 6836* (MO); *Stevens 7020* (MO); Caño Majagua, *Stevens 6924* (BM, MO); vicinity of Waní including Río Ulí, 90-110 m, *Stevens 7328* (MO); *Stevens 7980* (BM, MO); sheer dogtooth limestone peak and plain on E side of rocks, Cerro Waylawas, 100-268 m, *Stevens 7394* (MO); *Stevens 7328* (BM, MO). Department unknown: Miranda Bodega at confluence of Tunkey and Murcielago creeks, 820 ft, *Englesing 1498* (F); without locality: *Tate 122* (K). COSTA RICA. Alajuela: Cuesta de la Vieja, entrée de la plaine du San Carlos, 750 m, *Biolley 960* (BR); Cote de la Calera de San Mateo, 850 m, *Brenes 3589* (F); San Rafael de San Ramón, *Brenes* 5925 (CR); Camino San Francisco y La Calera de San Ramón, *Brenes 6482* (F, NY); San Pedro de San Ramón, *Brenes 6579a* (NY); disturbed margins of primary forest along rd between Cañas and Upala near Río Zapote, 100 m, *Croat 36396* (MO); Santa

María National Park, near park headquarters (Hacienda Santa María), 800-900 m, *Liesner 4556* (MO); Villa Quesada, Canton San Carlos, 825 m, *Smith P2575* (F, GH); disturbed margins of primary forest 2 km N of Bijagua 450 m, *Utley & Utley 3926* (DUKE, GH, MO, US); vicinity of Aguas Claras, *Utley & Utley 3982* (DUKE); disturbed primary forest, 4 km S of Bajo Rodriguez, 300-400 m, *Utley & Utley 4623* (CR, DUKE, MICH, MO, NY); 9 km N of Río Naranjo along rd to Upala, 400 m, *Utley & Utley 5340* (DUKE, F, US); remnant forest and roadbanks 27.6 km NE of Liberia on Camino Santa María, 800 m, *Utley 5902* (CAS, CR, DUKE, F, MEXU, US); 31.3 km N of Liberia on roadbanks along Camino Santa María, 700 m, *Utley 5906* (B, C, DUKE, F, GH, MO, NY, US); remnant forests and roadbanks 4-5 km N of Bijagua, 500-600 m, *Utley 5930* (BR, CAS, DUKE, TEX). Cartago: steep slopes above Río Reventazón and below IICA near Turrialba, 700 m, *Burger 3874* (F); *Carlson 3346* (in part) (F); Pejivalle, 900 m, *Standley & Valerio 46771* (US); Tuis, *Tonduz 9827* (CR, G); *Tonduz 10141* (US); *Tonduz 10148* (US); lieux frais à Las Vueltas, Tucurrique, 635 m, *Tonduz 13157* (BM, CR, M, P, US); Reventazón River, 10 km SE of Turrialba, 600 m, *Williams 19563* (US). Guanacaste: potreros near farmhouse at Hacienda Santa María and source of Río Liberia, 680-780 m, *Dodge & Thomas 6329* (GH, MO, US); forest above Hacienda Tenorio, *Schubert 1057* (F); *Schubert 1077* (F); Tilarán, 500-650 m, *Standley & Valerio 44279* (F); *Standley & Valerio 44397* (US); mountains about 5 km E of Tilarán, above Laguna de Arenal, 900-1000 m, *Williams & Williams 24583* (F, US). Heredia: Puerto Viejo de Sarapiquí, *Schubert 1290* (F); *Schubert 1350* (A, US). Limón: La Concepción, Llanuras de Santa Clara, 250 m, *Smith 6514* (US); Río Pacuare, about 15 km W of Moravia, 800 m, *Williams 19473* (US). Puntarenas: 1 km SE of Río Claro along NE side of Interamerican Hwy, 20-30 m, *Burger & Mata 4816* (F); rocks on coast near Quepos, *Foster 2662* (US); San José: bassin du Diquis, bord d'un ruisseau à Buenos Aires, 250 m, *Tonduz 3908* (BR, US). PANAMA: Chiriquí: Burica Peninsula, San Bartolo Limite, 21 km W by NW of Puerto Armuelles, 400 m, *Busey 465* (F, MO, NY); Veraguas: San Lorenzo, *Seemann 1660* (BM, K). COLOMBIA. Cauca: 77 km W of Cali, rd to Buenaventura, Valle del Cauca, 1000 ft, *Barkley 38C* (US); *Barkley & Bouthilette 38C633* (US); Río Sucio, SW of Tambu, 1100 m, *Haught 5264* (US); Cordillera Occidental, vertienti oriental El Tambo, Corregimiento de López, 1750 m, *Idrobo & Fernandez 233* (US). Cundinamarca: Pacho-La Palma Hwy, 1000 m, *Haught 6018* (US). El Valle: Dagua Valley, 300- 400 m, *Killip 11439* (K, US); Río Dagua, Cisneros, 300-500 m, *Killip 35577* (US). Santander: above Bucaramanga on rd to Pomplona, 8000 ft, *Barkley 38C246* (US); Río Suratá valley between Bucaramanga and El Saboncillo, 800-1500 m, *Killip & Smith 16351* (US). Uraba (Antioquia): bosques de Dadeiba, 450 m, *Uribe 1466* (US); Dabeiba, sito "La Cerrazón", 400 m, *Uribe 2059* (US) Department unknown: dry roadside 5 km N of Consaca, 7000 ft, *Barkley & Bouthillette 38C748* (US); stream S of Consaca, 5500 ft, *Bouthillette & Mullen 38C747* (US); deep rocky valley with steep slopes near La Plata, *Epple 360* (US); Campo Allegro, Calima Valley, *Robinson 379* (US); narrow canyon by falls 77 km S of Popayan rd to Pasto, 3200 ft, *Barkley & Mullen 38C730* (US).

21. *Begonia plebeja* Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 8. 1852. TYPE: COSTA RICA: In monte Aguacate 11/46. *Oersted s.n.* (Lectotype: C!; isolectotype: B!).

Gireoudia plebeja (Liebm.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

Begonia leptophylla C.DC., Bull. Herb. Boiss. II. 8: 319-320. 1908. TYPE: NICARAGUA: Ile de Zapatera, fentes des rochers 40 m, *Lévy 197* (Holotype: G!; isotypes: C!, LG!, P!), *nom. illeg.* Art. 64.

Begonia ripicola C.DC., Bull. Herb. Boiss. II. 8: 314. 1908. TYPE: COSTA RICA: Buissons au bord du Río Torres à San Francisco de Guadaloupe, 1170 m, *Tonduz 9825* (Holotype: BR!; isotypes: BR! [2 sheets]).

Begonia tenuipila C.DC., Bull. Herb. Boiss. II. 8: 315. 1908. TYPE: COSTA RICA: Bords d'un ruisseau à Nicoya, *Tonduz 13515* (Holotype: US!; isotype: CR!).

Begonia fissurarum C.DC., Smithson. Misc. Coll. 69(12): 2. 1919. Substitute name for *B. lepto-*

phylla.

Begonia uvana C.DC., Smithson. Misc. Coll. 69(12): 4. 1919. TYPE: PANAMA: Veraguas, Isla de Uva, Contreras group, *Pittier 5109* (Holotype: US!; isotype: G!-fragment, NY!).

Begonia plebeja Liebm. var. *kennedyi* Ziesenhenne, The Begonian 26: 61-62. 1959. TYPE: PANAMA: Old Panama, *Rose & Rose 18508* (Holotype: US! U.S.N.H. 761196; isotype: NY!).

Begonia tenuipila var. *kennedyi* (Ziesenhenne) Ziesenhenne, The Begonian 44: 100. 1977.

Acaulescent herbs; *rhizomes* repent, generally much branched, light green but soon becoming dark ferrugineous, 2.3-8 (18) cm long; internodes very short, 2-6 (12) mm X 0.8-1.8 (2.5) cm, moderately to densely villous with whiplash trichomes intermixed with coarse barbate, basally rounded or flattened trichomes 2-3 mm long. *Leaf blades* simple, subcoriaceous but membranaceous to chartaceous when dry, light to dark green throughout or occasionally maculate, oblique to transverse, broadly oblong-elliptic, suborbicular, ovate or obovate, 6-18 (23) X 4-13 (18) cm, basally broadly shallowly cordate to deeply narrowly cordate with lobes overlapping, apically attenuate-acuminate to abruptly short acuminate or infrequently acute, marginally variable, infrequently lobed but occasionally with a broad but shallow apically obtuse to acute lobe opposite the petiole, often dentate, cuspidate or doubly dentate at ends of major nerves, ciliate and generally denticulate, glabrous to very sparsely pilose above, especially on principal nerves, but sparingly to moderately pilose or glandular-pilose throughout beneath, becoming more dense on major nerves, palmately 7-11-nerved. *Petioles* light green but frequently suffused with pink and often deep red distally, (2.5) 4-26 cm X (0.5) 1-5 (6) mm, lenticellate, sparingly to moderately pilose with whiplash trichomes 1-3 mm long, rarely glabrous. *Stipules* persistent, translucent light pink but soon drying to tan, very thick basally and along the conspicuous nerves, intercostal regions hyaline and often disintegrating with age, generally adpressed to the rhizome, asymmetrically triangular, (0.4) 0.9-1.6 (2) X 0.5-1.2 (1.4) cm, unkeeled or only weakly keeled distally, apically attenuate-acuminate, marginally entire, glabrous to glandular, pilose or glandular-pilose throughout. *Inflorescences* axillary but often appearing apical when arising from subapical regions before new leaves develop, asymmetric to strongly asymmetric or unilateral, laxly to densely cymose, few- to many-flowered, 3-12 (18) cm diam. *Peduncles* light green to pink, 5-35 cm X 1-4 mm, sparingly to densely pilose, often glabrate with age. *Bracts* caducous, the lowermost subequal, navicular, ovate, oblong or obovate, 5-9 X 3-6 mm, apically acute to obtuse, marginally ciliate and ciliate-denticulate to ciliate-serrulate. *Staminate flowers*: pedicels 4-16 mm long, sepals white to light pink, elliptic to ovate, obovate or suborbicular, 4-8 (13) X 4-8 (10.5) mm, glabrous to sparingly glandular; petals wanting; stamens 11-21 (24); filaments 0.3-1 mm long, borne on a raised torus; anthers oblong to oblong-obovate, 1.3-2 X 0.5-0.8 mm. *Pistillate flowers*: pedicels 6-13 (20) mm long; bracteoles well-developed, submembranaceous, elliptic, ovate or broadly obovate, 3.5-7 (10) X 2-9 (11) mm, apically obtuse, marginally laciniate to ciliate and ciliate-serrulate; sepals colored like staminate sepals, orbicular, suborbicular or transversely elliptic, 4.5-9 X 5.5-8.5 mm; petals generally wanting, but when present, 1, caducous, oblanceo-

late, 6.5-1 mm; ovary 5.5-9 (13.5) mm long, glabrous to glandular-pilose throughout; styles 3, 2.5-3.5 mm long, connate briefly basally; stigmas lunate. *Capsules* with pedicels 0.8-2.8 (3.2) cm long, trilocular, (9) 11-15 (19) mm long; locule chambers externally appearing elliptic to oblong or slightly obovate, 6-14 X 4-8 mm; wings 3, unequal, the largest broadly asymmetrically triangular or obliquely ovate, rarely broadly oblong, 8-16 X 8-17 mm, apically oblique, acute to obtuse or truncate, the second asymmetric and broadly, shallowly triangular to lunate, 4-10.5 X 6.5-16 mm, apically acute to obtuse, the third marginiform or occasionally equal or subequal to the second wing.

DISTRIBUTION AND HABITAT: Central Mexico to central Panama where it occurs from 40 m to 1500 m. *Begonia plebeja* is a frequent inhabitant of tropical deciduous forests where it often grows epiphytically or saxicolously in exposed locations. Populations in seasonally dry areas like the Valle Central in Costa Rica are deciduous, but populations from areas where the environment is less harsh may show variation in this character. This is suggested by the continued presence of leaves on some late fruiting specimens. When individuals from populations known to be deciduous are maintained under a constant environment, they will continue to drop their leaves each winter (Fig. 18).

FLOWERING: Most profuse towards the end of the rainy season, October to January, with populations in northern Central America and Mexico commencing flowering in October while populations from southern Central America flower slightly later, late November to December.

DISCUSSION: Liebmann (1852) based his description of *B. plebeja* upon Oersted collections from Nicaragua and Costa Rica. The collections, which are clearly conspecific, differ slightly from each other in only one noticeable character, the nature of the leaf margin. The Costa Rican element has ciliate and strongly dentate leaves, with the dentations becoming almost cuspidate, while the Nicaraguan specimen has leaves with margins that are ciliate, denticulate or at best, weakly dentate. Weighing this character heavily, Ziesenhenne (1977) maintains that the two elements represent two distinct species, *B. tenuipila* and *B. plebeja*. As a result of this, Ziesenhenne (1977) emended Liebmann's original description of *B. plebeja* and, not recognizing the necessity of designating a lectotype, considered the Oersted collection from Nicaragua the type because it was mentioned first. Of the two collections, the Oersted specimens from Costa Rica agree more closely with Liebmann's protologue than does the Nicaraguan collection. I, therefore, am selecting Oersted's Costa Rican collection at Copenhagen as the lectotype for *B. plebeja*.

At the time Casmir de Candolle (1908) described *B. tenuipila*, which he thought might have peltate leaves, he also described two other taxa, *B. ripicola* and *B. leptophylla* which are conspecific with *B. plebeja*. The element represented by *B. ripicola* is very similar to that which formed the basis of *B. tenuipila*, differing largely in mature plant size. The collection Candolle used to describe *B. leptophylla* (*Levy 197*) has small, only weakly dentate and denticulate leaves and depauperate inflorescences. Another taxon, *B. uvana* was based on *Pittier 5109* from the Isle de Uva; its most distinctive features are capsules with wings differing slightly in form from the typically triangular primary wings on capsules of *B. plebeja*. However, this character hardly warrants either specific or infraspecific

recognition. *Begonia barsalouxii* has been treated as a synonym of *B. plebeja* (Smith and Schubert, 1961), but this taxon is potentially of hybrid origin and is being treated under doubtful and excluded species.

When Ziesenhenne described *B. plebeja* var. *kennedyi* and later transferred it to *B. tenuipila*, he cited the type as "Mr. and Mrs. J. N. Rose, No. 19809 overwritten No. 18508. June 1914, United States National Herbarium No. 761196" (Ziesenhenne, 1959; 1977). Examination of U.S.N.H. 761196 revealed that the Rose & Rose collection was incorrectly cited; it is *18509* with the 9 crossed out so that it reads *18508*. Variety *kennedyi* is a reflection of variation among individuals in a population. Ziesenhenne (1959) revealed this when he cited as a paratype, *Rose & Rose 18508* from NY, but excluded another sheet of the same collection at NY, saying it represented a different species. Both NY specimens are clearly from the type series and unequivocally conspecific.

Begonia plebeja is a well-defined species that is readily separated from other species by its rhizomes with thick, persistent triangular stipules, staminate flowers with 11 to 24 stamens, bracteolate pistillate flowers with lunate stigmas, characteristic triangular capsular wings and pubescence. It is variable in several characters, leaf margination, cyme symmetry, and position of pistillate bracteoles. Like *B. manicata* and *B. sericoneura*, in *B. plebeja* leaf margination varies throughout its distribution. Leaves of plants from Mexico to Honduras and Nicaragua generally lack the strongly dentate, almost cuspidate margins frequently encountered in Costa Rican and Panamanian collections of this species. Although cymes of *B. plebeja* are often unilateral, they are also often only moderately asymmetric and individuals with these inflorescences have been misidentified as *B. sericoneura*. The bracteoles are typically borne on or immediately beneath the ovary in *B. plebeja*, but in some individuals they are situated further down the pedicel (*Standley 79362, Oersted s.n.*).

In its thick rhizomatous habit, pubescence, bracteoles and generalized stigma and capsular form, *B. plebeja* shares characters with both *B. sericoneura* and *B. crassicaulis* and has been placed in the sericoneura species group. Like the other species in the group, *B. plebeja* has an indument of whiplash trichomes. Although *B. plebeja* has repent rhizomes with thick, generally appressed triangular stipules and *B. sericoneura* is characterized by erect or ascending rhizomes with ovate or triangular stipules with hyaline intercostal regions, the taxa have frequently been misdetermined because inflorescence asymmetry was employed to distinguish between them. This problem is pursued further under *B. sericoneura*. *Begonia plebeja* also differs from *B. sericoneura* in its sparingly to moderately pilose petiolar indument, smaller staminate sepals and fewer stamens. Although both species are adapted to survive in seasonally dry habitats, *B. plebeja* favors habitats that are much more harsh during the dry months and is one of only a few species in the section to occur in tropical deciduous forests. *Begonia plebeja*, like *B. crassicaulis*, is often deciduous, but differs from *B. crassicaulis* in its repent rhizomes, oblique to transverse unlobed leaves, often smaller sepals and unequal capsule wings (Table 10).

SPECIMENS EXAMINED. MEXICO. Chiapas: wooded slope 2 mi S of Tuxtla Gutiérrez along rd to Villa Flores, Municipio of Tuxtla Gutiérrez, 2800 ft, *Breedlove & Raven 13319* (DS, US); rocks on gradual heavily wooded slope 17 km N of Tuxtla Gutiérrez along rd to El Sumidero, 4000 ft, *Breedlove 14004* (DS, MEXU, MICH,

US); steep walled canyon with Tropical Deciduous Forest above El Chorreadero, Municipio of Chiapa de Corzo, 800 m, *Breedlove & Thorne 20492* (DS); *Breedlove & Thorne 20494* (MO); El Sumidero, 22 km N of Tuxtla Gutiérrez, 1350 m, *Breedlove & Smith 21553* (DS); small streams 6-8 km NE of Huixtla along rd to Motozintla, Municipio of Huixtla, 200 m, *Breedlove 22537* (DS); *Breedlove 28557* (DS); steep canyon, 15 km SW of Suchiapa along rd to Villa Flores, Municipio of Suchiapa, 750 m, *Breedlove 28228* (CAS); ravines 13 km N of Arriaga along Mexican Hwy 195, Municipio of Arriaga, 830 m, *Breedlove 28268* (DS, MEXU, MO); steep ravine, 20 km W of Ocozocoautla, Municipio of Ocozocoautla de Espinosa, 100 m, *Breedlove 28374* (DS); 5 km W of Rizo de Oro, Municipio of Cintalapa, 900 m, *Breedlove 36708* (DS); 58 km S of Mexican Hwy 190 on rd to Nueva Concordia, Municipio of Villa Corzo, *Breedlove 37545* (DS); 13 km S of Ocozocoautla, Municipio of Ocozocoautla de Espinosa, 900 m, *Breedlove 37839* (DS); Cerro Vernal, seasonal evergreen forest, 21 km S of Tonalá, Municipio of *Tonalá*, 750 m, *Breedlove 38097* (DS); 10 mi NE of Escuintla just above El Triunfo, 300 m, *Croat 43857* (MO); Río Quilco, Soconusco, *H.T.G. 43* (DS); Río Grijalva, along rd to Acala at Nandabure, Municipio of Acala, 1600 ft, *Laughlin 2806* (DS, US); rd from Acala to Venustiano, Municipio of Venustiano Carranza, *Laughlin 2901* (DS, US); Esperanza, Municipio of Escuintla, *Matuda 17010* (DS); Mt. Ovando, Municipio of Escuintla, *Matuda 17045* (DS, MEXU); Turquia, Municipio of Escuintla, *Matuda 17077* (NY); wet forest, Zacatonal, Acacoyagua, 1200 m, *Matuda 18349* (US). Guerrero: Vallecitos, Distrito de Montes de Oca, *Hinton 11474* (MICH, NY); Barranca Limo, Temisco, Sierra Madre del Sur, N of Río Basas, Distrito Adama, 400 m, *Mexia 8709* (CAS, F, GH, MO, NY, UC, US); Temisco, Barranca Julia, Sierra Madre del Sur N of Río Balsas, Distrito Adama, 350 m, *Mexia 8730* (CAS, F, GH, MO, NY, UC); cutover hillside with limestone outcrops at km 338, hwy to Acapulco, 3000 ft, *Moore & Wood 4721* (A); streamsides, vicinity of km 284 below Tierra Colorado, hwy to Acapulco, 7000 ft, *Moore 5266* (BH, BM, GH, UC, US). Jalisco: steep wooded hills above river 11 mi N of bridge of Río Cihuatlán on rd from Santiago, Colima to Durazno, Jalisco, 500-550 m, *McVaugh 15976* (MICH, US); 16 mi SW of Autlán, seaward slopes 6.5 mi below hwy pass, 750 m, *McVaugh 19954* (MICH); barranca of Tepic, *Pringle 4553* (BM, GH, M, MEXU, MO, MSC, NY, P, UC, US). México: Limones, Distrito Temascaltepec, 910 m, *Hinton 2518* (GH, US); Palmar, Distrito Temascaltepec, *Hinton 7045* (GH, US); Ixtapan, Distrito Temascaltepec, *Hinton 8550* (US). Michoacán: Aquila, Distrito Coalcomán, 300 m, *Hinton 12599* (MICH, NY, UC); Rancho Viejo, Distrito Apatzingan, 530 m, *Hinton 15191* (MICH, NY, US); Aguililla, Distrito Apatzingan, 950 m, *Hinton 15294* (DS, MICH, NY, US); Aquila, Distrito Coalcomán, 750 m, *Hinton 16001* (K, MICH, UC, US); Hinton 16013 (US); *Hinton 16020* (MICH, US); *Hinton 16029* (K, MICH, UC, US); small tributary of Río Carlos E of road camp 75 km from El Temascal on rd to Huetamo, 750-850 m, *Moore, Hernandez & Porras 5669* (BH, BM, GH, UC). Michoacán and Guerrero: El Calabazal, 150 m, *Langlassé 467* (GH, P). Nayarit: Mirador del Aquila, 14 NW of Tepic, 450-550 m, *McVaugh 19006* (MICH). Veracruz: Limestone rocks near Remudadero, *Purpus 10578* (NY, US); Barranca de Remudadero, *Purpus s.n.* (DS, US); Zacuapan, *Purpus s.n.* (B). Without locality, *MacDougall C-27* (US). GUATEMALA. Chiquimula: Taco creek and rocky hills about 1 mi W of Chiquimula, *Clover 9205* (MICH); rocks in dense woods along divide above El Rincón, 870 m, *Standley 74669* (F); rocky outcrops along gorge of Río Chiquimula, between Santa Bárbara and Petapilla, 4-6 mi N of Chiquimula, 350-420 m, *Steyermark 30274* (F, GH); Socorro Mountain between Finca San José and Montaña Nube, 1200-1700 m, *Steyermark 30963* (F, GH). Guatemala: Estancia Grande, 600 m, *Standley 59222* (F). Jalapa: rd between Jalapa and San Pedro Piñula, 1400-1800 m, *Standley 77030* (F, GH); mountains about Chahuité, NW of Jalapa, 1650 m, *Standley 77474* (F). Jutiapa: Cuesta de la Conora, between San José Acatempa and Río de Los Esclavos, 900-1000 m, *Standley 60619* (F); Jutiapa, *Standley 75304* (F, GH); El Barrial, E of Jutiapa, 800 m, *Standley 75785* (F); quebrada above Ovejero on rd between Monjas an El Progresso, 1400 m, *Standley 77602* (F); wet thicket near El Molino, 600 m, *Standley 78451* (F, GH). Retalhuleu: San Martín, 1250 ft, *Shannon 186* (US). Sacatepéquez: Las Lajas, *Standley 58290* (F); Santa Rosa: Buena Vista, 5500 ft, *Heyde & Lux 4191* (B, NY, US); hills E of Cuilapa along stream supplying city water, 900-950 m, *Standley 78135* (F, GH); El Molino, 600 m, *Standley 78338* (F); Río Panal, lower slopes of Volcán de Tecuamburro rd between Cuilapa and Chiquimulilla, *Standley 78570* (F); Guazacapán, 200 m, *Standley 78676* (F); region of La Sepultura, *Standley 79362* (F, GH); Chiquimulilla, 325 m, *Standley 79693* (F). Suchitepéquez: Cuyotenango, 1100 ft, *Shannon 279* (US); Río Madre Vieja, above Patulul, 450 m, *Standley 62232* (F). Zacapá: near divide on rd between Zacapá and Chiquimula, *Standley 73820* (F); trail between Río Hondo and waterfall, Sierra de las Minas, 250-400 m, *Steyermark 29412* (F); *Steyermark 29453* (F). Department unknown: Mazatenango, *Bernoulli & Cario 2863* (K); Caballo Blanco, *Kellerman s.n.* (US). HONDURAS. Copán: Copán river, 3 km to Santa Rita on rd to La Entrada, 700 m, *Molina & Molina 24723* (F). El Paraíso: drainage of the Río Yeguare, 1000

m, *Molina 4123* (F); Finca Sta. Emilia, Montaña de Apauhis, *Molina 5092* (F); wet thicket near Yuscarán, 960 m, *Standley, Williams & Molina 1180* (F); *Standley, Williams & Molina 1187* (F); Río California, base of Sierra de la Villa Santa, 720 m, *Standley 28077* (F). Lempira: Quebrada Banaderos cerca de Lepaera, 1200 m, *Molina 13005* (F). Morazán: Suyapa, 1100 m, *Molina 550* (F); drainage of Río Yeguare, 950 m, *Molina 1540* (F); Río Guacerique between Los Laureles and Las Tapias, NW of Tegucigalpa, 1000 m, *Molina 18579* (F, GH); Uyuca, 1238 m, *Rodriguez 1590* (F); El Zamorano, 780-900 m, *Standley 179* (F); *Standley 12519* (F); rd from El Zamorano toward San Antonio de Oriente, 835-950 m, *Standley 14243* (F); Rio de la Orilla, SE of El Zamorano, base of Cerro Majicarán, 759-800 m, *Standley 14420* (F); above El Jicarito, 900 m, *Standley 14825* (F); Río de la Orilla, SE of Zamorano, 750-800 m, *Standley 24697* (GH, US); 20 km S of Sabana Grande, 500 m, *Williams & Molina 10968* (GH); drainage of Río Yeguare, 2 km NW of El Zamorano, 850 m, *Williams & Molina 14790* (F). Santa Bárbara: Llano del Conejo, 1 km de Santa Bárbara, 300 m, *Molina 3670* (F). EL SALVADOR. Ahuachapán: rd (El Impossible) to Tacuba, 2-3 mi NW of San Francisco Menéndez, 500 m, *Croat 42094* (MO). Chalatenango: Dulce Nombre de María, *Bernhardt 5150* (UC). San Salvador: San Salvador, *Calderón 66* (US); *Standley 19145* (NY, US); San Vincente: Volcán de San Vincente, 1200-1500 m, *Standley 21485* (US). Sonsonata: Pedregal de San Isidro, ca 3 mi S of Lake Coatepeque on Hwy 8, 850 m, *Croat 42255* (MO). Department unknown: Sierra de Conchagne, Gulf of Fonseca, *Barclay 2693* (BM). *NICARAGUA*: Estelí: Río Estelí, 900 m, *Molina 23009* (F, NY); Rio Esteli, Guava, *Molina 23133* (F, NY); *Williams & Molina 42358* (F); wooded canyon below waterfall, Salto de Estanzuela, 10 km S of Esteli, 1000 m, *Neill 1185* (MO). Granada: Volcán Mombacho, *Dudley & Moore 1985* (MO, US); *Nichols 2212* (DUKE, NY, UC, US). Managua: Managua, *Garnier 77* (US); 4 km from Hwy 12 near bridge over Río Aduana, 50-100 m, *Stevens 5397* (MO). Masaya: SW slope of Volcán Santiago near Masaya, 300-450 m, *Maxon 7713* (US); Masaya Lake, *Nichols 134* (BM, MO, NY, US, US); *Neill 1019* (MO). Nueva Segovia: river bed in deep ravine 3 km W of Ocotal, *Nichols 789* (US). Department unknown: In monte El Viejo, *Oersted s.n.* (C). COSTA RICA. Alajuela: Río Poás, del Cacao de Alajuela, *Brenes s.n.* (NY); La Palma de San Ramón, *Brenes 5810* (CR, F, NY); San Miguel de San Ramón, *Brenes 6420* (CR); Colinas de San Pedro de San Ramón, *Brenes 6446* (CR); Carrillos du Poás, Camino Viejo al Río Poás, *Brenes 17392* (CR, F). Guanacaste: Río Guapote, Santa Rosa National Park 100-250 m, *Liesner 4510* (MO); rocks along river, 10 km SW of Curime and 15 km SW of Nicoya, *Liesner 5015* (CR, MO); forested slope of escarpment above Bahia de Salinas, about 5 km S of La Cruz, *Williams, Molina & Williams* (F). Puntarenas: Cabo Blanco Nature Reserve on S tip of Nicoya Peninsula, 0-200 m, *Burger & Liesner 6573* (CR, F, NY). San José: 1 km al NW of Villa Colón, *Jiménez 1317* (CR, NY); Río Virilla à la Uruca près San José, 1100 m, *Pittier 741* (BR); forêts de Boruca, *Pittier 4667* (G, BR); Río Virilla about 1 km S of Santo Domingo, *Taylor 17529* (NY, US); *Taylor 17324* (NY); Río Virilla, 1100 m, *Tonduz 7032* (K, BM, US); San Francisco de Guadaloupe, *Tonduz 9828* (BR). PANAMA. Canal Zone: between Madden Dam and Saddle II near Alahuela, 90-100 m, *Dodge, Steyermark & Allen 16503* (MO); westerly arm of Quebrada Salamanca, 70 m, *Dodge 17008* (BM, BR, C, DS, MICH, UC); banks of Quebrada Fea, Qda. Pura and Cañon of Río Chagres, 700-100 m, *Dodge & Allen 17408* (MO); telephone trail between Río Indio Hydrographic Station and Natural Bridge of Río Puente, *Dodge & Allen 17482* (MO); Madden Dam, *Dwyer 3045* (MO); Cerro Galera, 2 km from Pacific Ocean near W boundary of Canal Zone, 350-400 m, *Gentry 6629* (MO, NY); rd between Transisthmian Hwy and Madden Dam, *Gentry 6682* (MO, NY); disturbed forest in vicinity of Madden Dam, *Lewis, Dwyer & Elias 33* (MO); *Lewis, Dwyer & Elias 34* (MO, US); headwaters of Río Casaya, 6 km E of Gamboa, *Nee 9020* (MO); dry limestone hills near Madden Lake, Sotto Caballo, *Smith, Smith & Arrauz 3324* (F, US); Las Cascades Plantation near Summit, *Standley 25683* (US); *Standley 25759* (C, US); *Standley 25781* (US); *Standley 29513* (US); Madden Lake, various trails beyond dam, *Witherspoon & Witherspoon 8808* (MO, NY). Chiriquí: mixed evergreen forest 5.5 mi S of Cerro Punta along cleared path in forest, *Graham 277a* (GH, MICH). Coclé: El Valle, 800-1000 m, *Allen 94* (F, GH, MO); rd to El Cope from Interamerican Hwy, *Burch, Oliver & Robertson 1384* (GH, MO). Darién: Río Chico, *Duke & Bristan 443* (MO). Los Santos: Río Guaniquito above El Cortezo, *Hammel 5308* (MO); *Hammel 5309* (MO); El Pavo bridge above Río Los Changuales, 10 km SW of El Cortezo, S part of Azuero Peninsula, 1500-2000 ft, *Hammel 5445* (MO); Playa Venando, 30 km E of Tonosi on Hwy 50, *Hammel 5476* (MO); vicinity of headwaters of Río Pedgal, 25 mi SW of Tonosi, 2500-3000 ft, *Lewis et al. 2908* (MO, UC); rd between Tonosi and Macaracas, *Oliver, Robyns & Verhoek 3569* (MO, UC); 11 mi N of Tonosi, *Tyson, Dwyer & Blum 2972* (MO). Panamá: Río la Maestra, 0-25 m, *Allen 58* (F, GH, MO); Isla Taboga, *Allen 1264* (F, GH, MO, US); shady roadside between Cañitas and El Llano, *D'Arcy 9410* (MO, US); rd between Panamá and Chepo, *Dodge et al. 16680* (MO); *Dodge et al. 16683* (BR, MO); streambanks in area around Pilote de Toro,

Folsom, Collins & Alonzo s.n. (MO); Taboga Island, Bay of Panama, *Howe s.n.* (NY); wooded ravine in M-area, San José Island, Perlas Archipelago, Gulf of Panama, *Johnston 83* (GH); *Johnston 207* (GH, MO, US); *Johnston 322* (GH, US); *Johnston 386* (GH, MO); *Johnston 436* (GH, MO, US); Chiman, 3-4 mi up Río Pasiga in semi-deciduous forest, *Kennedy 1027* (DUKE); Taboga Island, *Killip 3167* (US); wet forest along Río Tapia, *Standley 26172* (US); *Standley 28288* (US); Taboga Island, *Standley 27966* (US); Juan Díaz, *Standley 30583* (US); Playa Grande, San José Island, *Tyson & Loftin 5095* (MO). Veraguas: Azuero Peninsula, 6 km SW of El Cortezo on slopes of Quebrada Los Changuales, 1500 ft, *Hammel 5340* (MO); *Hammel 5341* (MO); Puerto Mutis, 12 mi S of Santiago, *Tyson 5187* (DUKE, MO). Without locality: *Duchassaing s.n.* (GH).

22. *Begonia conchifolia* A. Dietr., Allg. Gartenzeit. 19: 258. 1851. TYPE: CENTRAL AMERICA: described from cultivated material grown at Berlin from seed sent by Warscewicz from Costa Rica (Holotype: presumably B, not seen and perhaps nonexistent).

Begonia scutellata Liebm., 1852. Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1852: 9. 1852. TYPE: COSTA RICA: In monte Candelaria, 6000 ft, February 1847, *Oersted s.n.* (Lectotype: C!; isolectotypes: B!, C!).

Gireoudia conchifolia (A. Dietr.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

Gireoudia conchifolia var. *scutellata* (Liebm.) Kl., Abh. Königl. Akad. Wiss. Berlin. 1854: 217. 1855.

Gireoudia conchifolia var. *warscewicziana* Kl., Abh. Königl. Akad. Wiss. Berlin. 1854: 217. 1855. TYPE: Locality unknown: described from material cultivated at Berlin (Holotype: presumably B, n.v.)

Begonia pumilio Standl., Ann. Missouri Bot. Gard. 27: 322. 1940. TYPE: PANAMA: Panamá: Cerro Campana, December 31, 1939, *Allen 2089* (Holotype: F!; isotypes F!, GH!, MO!, US!)

Begonia conchifolia var. *rubimacula* Golding, The Begonian 40: 189. 1973. TYPE: COSTA RICA: Cartago, El Muñeco, south of Navarro, 1400 m, February 8-9, 1924, *Standley 33417* (Holotype: US!)

Herbaceous perennials: *rhizomes* repent, usually much branched, crimson to light green but pink-brown to ferrugineous when dry, 1.5-9 cm long; internodes very short, 1-10 (15) X (1.5) 2.5-6 (11) mm, lenticellate, glabrous; nodes squamose, with broad fimbriate-laciniate scales at bases of petioles and stipules. *Leaf blades* simple, succulent when living but chartaceous when dry, oblique, symmetric to weakly asymmetric, ovate to suborbicular, 2-9 (14) X 1-8 (10) cm, basally peltate, apically attenuate-acuminate to abruptly short acuminate or infrequently acute, marginally irregularly denticulate-serrulate to obsoletely crenulate or undulate, nitidous and sparingly pilose above and beneath, except for principal nerves below which are strongly tomentose-lanate especially when immature, 6-9-peltinerved. *Petioles* maroon to light green, (2) 5-27.5 (32.5) cm X 0.3-3 (4) mm, moderately to densely tomentose-lanate when immature, but only sparingly to moderately so at maturity, with spreading to antrorsely spreading whiplash trichomes 0.1-2 mm long, often with glandular trichomes intermixed. *Stipules* persistent, translucent light green to pink-red when living, asymmetrically broadly to narrowly ovate-triangular, 6-15 X 2-9 mm, weakly to strongly keeled, apically acute to acuminate, marginally entire, sparsely pilose throughout but only the

keel frequently laciniate-fimbriate. *Inflorescences* typically exceeding the foliage, weakly to strongly asymmetric, densely cymose, few- to many-flowered, (1) 2-10.5 (17.5) cm diam. *Peduncles* green to red-pink, (2) 5-27.5 (32.5) cm X 0.3-2.5 (4) mm, sparingly pilose to densely tomentose, with minute glandular trichomes interspersed. *Bracts* deciduous, pink to red-pink, the lowermost naviculat, broadly elliptic to ovate or obovate, 2.5-8 (11) X 2-9 mm, apically rounded, marginally entire basally, becoming ciliate-serrulate to ciliate-denticulate distally, sparsely pilose throughout. *Staminate flowers*: pedicels 3-9 (13) mm long; sepals white to pale or deep pink externally, suborbicular to elliptic, 3.5-6.5 X 2.8-6.5 (8) mm, glabrous; petals generally wanting but when present, 1, oblanceolate, 6 X 2.5 mm; stamens 6-13; filaments 0.3-1.3 (1.9) mm long, borne on a raised torus; anthers oblong to narrowly obovate, 0.6-1.5 X 0.3-0.8 mm. *Pistillate flowers*: pedicels (3) 5-9 (11) mm long; bracteoles subpersistent, white to green-white, frequently suffused with pink and infrequently dark pink-red, membranaceous, suborbicular to broadly obovate or transversely elliptic, 3-7 X 2.5-8 (9) mm, apically obtuse, marginally weakly ciliate-denticulate, sparingly glandular-pilose externally; sepals colored like staminate sepals, broadly elliptic to obovate or suborbicular, 2.5-7 X 2.2-6 mm, glabrous; petals wanting or 1, oblanceolate, 5 X 2 mm; ovary light green to white, frequently suffused with pink, 4-6.5 mm long, glabrous or sparingly covered with minute glandular trichomes; styles 3, 1.5-1.6 mm long, connate 1/3-1/2 their length; stigmas lunate. *Capsules* with pedicels 5.5-13 (16) mm long, trilocular, 4-10 mm long; locule chambers externally appearing suborbicular to broadly ovate or elliptic, 3-6 (8.5) X 3-7.5 mm; wings 3, subequal, the largest asymmetrically lunate to broadly but shallowly lunate-triangular, 3-7.5 X 3.5-10 mm, apically obtuse, the second asymmetrically lunate-triangular, 2-7 X 4-10 mm and third subequal to the second or marginiform.

DISTRIBUTION AND HABITAT: *Begonia conchifolia* occurs in Costa Rica and Panama between 550-2000 m elevation. In Costa Rica it is most abundant in premontane and lower montane wet forests and transition areas between premontane forests and tropical wet forests. *Begonia conchifolia* forms small, highly local populations and is often epiphytic on lower portions of tree trunks and saxicolous on steep rock faces where other vascular plants have not established. It is rarely successful on open roadbanks unless they are rocky or highly eroded (Fig. 15).

FLOWERING: Peak period is from December to April.

DISCUSSION: *Begonia conchifolia* is immediately recognizable by its small size, succulent peltate leaves, tomentose-lanate indument, densely cymose inflorescences, stamen number, bracteolate pistillate flowers with lunate stigmas, small capsules with subequal, shallowly lunate to lunate-triangular wings.

Both *B. scutellata* and *B. pumilio* are conspecific with *B. conchifolia*. The relationship between *B. scutellata* and *B. conchifolia* was first recognized by Klotzsch (1854, 1855), while Smith and Schubert (1958) treated *B. pumilio* as a synonym of *B. conchifolia*. The Oersted collection gathered in February 1847 at Copenhagen was selected as the lectotype for *B. scutellata*.

The petioles and peduncles of *B. conchifolia* are often deep pink or red-pink as are the bracteoles and sepals externally. This frequently appears dependent upon exposure since individuals from open, sunny locations are often

more highly pigmented than their counterparts from shaded areas. Unlike several other species in the section, the leaves do not become deeply suffused with anthocyanins when individuals grow in exposed sites. An attractive form of *B. conchifolia,* recently described as var. *rubimacula,* has a red spot on the blade above the petiole insertion. While this trait has been observed in *B. conchifolia* only on plants from the vicinity of Muñeco and Navarro, it is common in populations of other species in sect. *Gireoudia,* including *B. plebeja* and *B. sericoneura.* When a population from Muñeco was sampled (*Utley 5877*), individuals possessing and lacking the trait were found growing side by side. Rather than representing a discrete morphological unit, which is largely geographically isolated from the typical form, var. *rubimacula* is an expression of intrapopulational variation and, although it is a horticulturally attractive form of *B. conchifolia,* does not warrant formal varietal recognition.

Like *B. strigillosa* and several other species in sect. *Gireoudia,* leaves formed immediately preceding the dry season are much thicker and more succulent than those formed at other times during the year. As *B. conchifolia* is not deciduous, this feature may be important in enabling this taxon to colonize habitats that would otherwise be inhospitable during several months with little or no rain.

Begonia conchifolia is considered to be a part of the sericoneura species group because of its indument of whiplash trichomes, bracteolate pistillate flowers and lunate or lunate-triangular primary capsule wings. Although its trichomes are whiplash, they are uniseriate basally, unlike those of other members of the group with multiseriate basal portions. *Begonia conchifolia* differs from all species in the group by its small, peltate leaves and few stamens. Unlike *B. crassicaulis* and *B. sericoneura, B. conchifolia* has a repent non-succulent rhizome, much smaller than the rhizomes observed on either of these taxa. It can also be differentiated from *B. sericoneura* and *B. crassicaulis* by its smaller capsules (Table 10). With the exception of rhizome orientation which is similar, *B. conchifolia* may be separated from *B. plebeja* by the same characters which are used to distinguish *B. conchifolia* from *B. crassicaulis* and *B. sericoneura. Begonia conchifolia* differs from other peltately leaved taxa in its smaller size, fewer stamens and bracteolate pistillate flowers (Table 7).

SPECIMENS EXAMINED: COSTA RICA. Alajuela: Alajuela, 2700 ft, *Alfaro 5780* (US); San Pedro de San Ramón, 900 m, *Brenes 3625* (CR); *Brenes 5379* (CR); La Palma de San Ramón y camino de La Palma, *Brenes 5941* (F, NY); Cerro de Pata de Gallo de San Ramón, 1200 m, *Brenes 11525* (CR, F); Cataratas de San Ramón, *Brenes 13434* (CR, F, NY); Santiago de San Ramón, *Brenes 21983* (F); near Río María Aguilar on rd to Laguna Hule, 900 m, *Lent 3238* (F); pasture along Río Gorrion, Bajos del Toro, 1500 m, *Lent 3767* (F, NY); near Río San Rafael, 2 km W of La Marina, Llanura de San Carlos, 550 m, *Molina et al. 17306* (F, US); Zapote de San Carlos, 2000 m, *Smith PC289* (F); Canton Alfaro Ruiz, Zarcero, 1500 m, *Smith RZ19* (US); *Smith 121* (US); Cataratas de San Ramón, 700 m, *Utley & Utley 4620* (CR, DUKE, F, US); along gravel rd to Colonia Virgen de Socorro, steep slopes above Río Sarapiquí, 700-800 m, *Utley & Utley 4691* (DUKE, GH, MEXU); Cordillera Central near San Juan de Laja about 15 km N of Zarcero, *Williams et al. 29285* (F, NY). Cartago: La Carpintera, vicinity of Tres Ríos, 1300-2000 m, *Allen 511* (GH, MO); approx. 2 km E of Peñas Blancas bordering Río Naranjo, 1300-1400 m, *Almeda, Nakai & Utley 3976* (CAS); Río Reventazón, Juan Viñas, Reventazón Valley, 1000 m, *Cook & Doyle 248* (US); Las Concaves, near Cartago, 1140-1260 m, *Cooper 12* (F, NY); disturbed forest 1.5 mi E of Cachí, *Croat 47073* (MO); *Croat 47078* (MO); N slope of Cerro Carpintera, above battlefield of Laguna de Ochomogo, 560-1700 m, *Dodge & Thomas 6154* (GH, MO); *Hernandez s.n.* (CR); on hillside overlooking Río Tambor, 3 km E of Cachí, 1300 m, *Lent 862* (F, US); forest high over Rio Reventazón, 950 m, *Lent 2489* (F, NY); woods near

Río Naranjo, Orosi, 1400 m, *Lent 4047* (F, MO); Agua Caliente, 3900 ft, *Smith 4817* (US); El Muñeco, S of Navarro, 1400 m, *Standley 33417* (US); Cerro de La Carpintera, 1500-1850 m, *Standley 34231* (US); Finca Las Concaves, 1200-1300 m, *Standley 41528* (US); Pejivalle, 900 m, *Standley & Valerio 46932* (US); Río Reventazón, N of Cartago, 1460-1650 m, *Standley & Valerio 49637* (US); El Muñeco on the Río Navarro, 1400-1500 m, *Standley & Torres 51696* (US); Tuis, 650 m, *Tonduz 11427* (US); between Navarro and Muñeco, 1150-1200 m, *Utley 5877* (B, DUKE, F, GH, MO, US); 2 km E of Cachí along road paralleling Río Naranjo, 200 m, *Utley 5881* (CAS, CR, DUKE, F, MEXU, TEX); 9-12.5 km E of Tuis along rd to Moravia de Chirripo, 800-900 m, *Utley 6012* (DUKE). Guanacaste: El Silencio near Tilarán, 750 m, *Standley & Valerio 44786* (US); *Standley & Valerio 44829* (US); La Tejona, N of Tilarán, 600-700 m, *Standley & Valerio 45884* (US). Heredia: vicinity of Río El Angel, between Vara Blanca and Cariblanco, valley of Río Sarapiquí, 900-1000 m, *Moore 6617* (BH, US); forest near Cariblanco, 850 m, *Williams 20253* (US). San José: Isidro de Coronado, *Alfaro 34006* (US); near San Antonio de Escazú *Barkley 41551* (US); below La Palma, Río Claro along trail to Guapiles, 1000 m, *Burger 4147* (CR, F); valley of Río Hondura (below La Palma), 1000 m, *Burger & Stolze 4908* (F, NY); Río Claro valley below La Palma, 1000-1200 m, *Burger & Liesner 6264* (F); Guadaloupe, near San José, *Greenman & Greenman 5431* (MO); wet woods near Aserrí, 5000 ft, *Hunnewell 16665* (GH); Cerro Pico Blanco, 4 km S of Escazú, 1900 m, *Lent 3988* (F); Cinchona, *Schubert s.n.* (F); vicinity of El General, 1040 m, *Skutch 2369* (GH, MICH, MO, NY, US); Cerro de Piedra Blanca above Escazú, *Standley 32437* (US); between San Pedro de Montes de Oca and Curridabat, 1200 m, *Standley 32766* (US); La Hondura, 1300-1700 m, *Standley 36484* (US); small stream 1 km SE of Patarra, *Taylor 17562* (NY); rocks along edge of Rio Torres at San Francisco de Guadalupe, 1100 m, *Tonduz 9852* (BR, CR, GH, US); between Cascajal and San Isidro de Coronado, 5000-5400 ft, *Utley 5711* (DUKE). San José and Heredia: Calle Yerbabuena, 5 km NE of San Isidro de Heredia, 1400 m, *Utley & Utley 4458* (BR, C, CAS, CR, DUKE, F, G, MICH, MO, NY, TEX, US); PANAMA: Coclé: N of El Valle de Antón, vicinity of La Mesa, 1000 m, *Allen 2297* (F, GH, US); *Allen 2925* (GH, MO); flat forested area below Cerro Pilon, *Croat 13463* (F, MO). Panamá: dirt road to Cerro Campana, 2300 ft, *Correa & Dressler 854* (MO); *Hutchinson & Dressler 2957* (UC); trail above FSU Field Station and area of field station at Cerro Campana, 750 m, *Kennedy, Sucre & Braga 2044* (MO); *Lewis et al. 3052* (DUKE, MO, UC); *Liesner 617* (MO, NY, USF); *Maas & Dressler 725* (MO); *Utley 5705* (DUKE, MO, US).

23. *Begonia fonsecae* Standl., Ceiba 3: 151. 1952. TYPE: HONDURAS: Morazán: vicinity of El Zamorano, 500 m, 14 May 1952, *Standley 29539* (Holotype: US!; isotype: F!).

Terrestrial herbs; *rhizomes* decumbent, fleshy; internodes very short, to 5 mm long and about 1.5 cm diam., densely villous with whiplash trichomes 3-5 mm long intermixed with narrow barbate, basally rounded or flattened trichomes and broader laciniate scales 3-6 mm long. *Leaf blades* simple, oblique, asymmetrically ovate, 13.5-15.5 X 8.5-11 cm, basally peltate but appearing shallowly cordate, apically attenuate-acuminate, marginally shallowly peltilobed at ends of principal nerves, dentate to doubly dentate, ciliate, moderately to densely tomentose-lanate above and beneath when immature, becoming less dense to glabrate with age, 8-10 peltinerved. *Petioles* 10.5-17.5 cm X 1.5-3 mm, densely tomentose-lanate when immature, but sparingly so or glabrate with age. *Stipules* persistent, asymmetrically broadly lanceolate or narrowly ovate, 1.1-2.2 X 0.7-1.2 cm, weakly to strongly keeled, apically acute, marginally entire, sparingly pilose to glabrous or the keel only fimbriate to lacerate. *Inflorescences* equal to or slightly exceeding the leaves, asymmetric or unilateral, few- to many-flowered, 4.5-6.5 cm diam. *Peduncles* 17-19 cm X 2 mm, sparingly tomentose but glabrate with age. *Bracts* caducous, the lowermost broadly ovate to elliptic, 1.2 X 0.7 cm, apically rounded to obtuse, marginally denticulate to serrulate, sparsely pilose with glandular trichomes intermixed. *Staminate flowers*: pedicels 4-7 mm long; sepals suborbicular to broadly ovate, 6.5-7 X 6.5-7 mm, glabrous to sparingly glandular; petals wanting; stamens 27-30; filaments 0.5-1.3 mm long; anthers weakly deflexed apically, oblanceolate to

narrowly obovate or oblong, 1.2-1.6 X 0.5-0.6 mm. *Pistillate flowers*: pedicels 10-16 mm long; bracteoles wanting; sepals white to light pink, obovate to suborbicular, 7-10 X 6-9 mm, sparsely glandular; petals wanting; ovary 0.7-1 cm long, sparsely covered with minute glandular trichomes; styles 3, 1-1.5 mm long, connate 1/3-1/2 their length; stigmas broadly lunate. *Capsules* not seen.

DISTRIBUTION AND HABITAT: *Begonia fonsecae* is known only from plants collected from cultivation on the grounds of the Escuela Agrícola Panamericana, El Zamorano, Department of Morazán, Honduras, 800 m elevation (Fig. 8).

FLOWERING: Flowering material was gathered in May, but Standley (1952) reported that this species blooms throughout the year.

DISCUSSION: According to Standley (1952), *B. fonsecae* was originally introduced into cultivation from plants collected along the Río Yeguare in an area known as Monte Redondo on the property of the Escuela Agrícola. Although both Standley and Molina collected extensively in the area, the type collection and several other Standley collections of cultivated plants remain the only available material of this rare species. With the exception of the holotype and isotype, the remaining Standley collections are at the Escuela Agrícola (EAP) and were unavailable for study. Originally, when Standley described *B. fonsecae,* he designated the specimen at the Escuela Agrícola as the holotype, but this specimen was subsequently transferred to the U.S. National Herbarium along with other types, including *B. barsalouxii* and *B. robustior,* in December 1956.

Begonia fonsecae is characterized by its rhizomatous habit, peltate, but basally pseudocordate leaf blades, tomentoselanate indument, ebracteolate pistillate flowers and lunate stigmas. Although capsules were lacking from *Standley 29539,* wing morphology was inferred from ovaries of mature pistillate flowers. The largest wing, which is broadly asymmetrically triangular, is reminiscent of the large wing of *B. sericoneura* or *B. plebeja* in form. In comparison to many other species, the secondary wings are well-developed even on flowering material and are broadly asymmetrically triangular. Staminate flowers on both specimens lacked plump, well-developed anthers at anthesis. When pollen from one anther was treated with cotton blue-lactophenol, all 702 grains counted were non-staining and presumably non-viable. Moreover, the vast majority of grains were shrunken or otherwise malformed. This unusually high level of non-viability has not been observed in any other species within sect. *Gireoudia* and warrants further investigation when more specimens are available before any thorough evaluation of the status of *B. fonsecae* can be presented.

Begonia fonsecae shares with *B. sericoneura* and *B. plebeja* its succulent rhizomes with persistent stipules, indument of whiplash trichomes, potentially similar capsules and lunate stigmas. Since whiplash trichomes are known only from several species in sect. *Gireoudia,* this suggests a potential affinity for *B. fonsecae* with members of the sericoneura species group, *B. plebeja* and *B. sericoneura.* The major differences between these taxa are in the peltinerved and weakly peltilobed leaves and ebracteolate pistillate flowers of *B. fonsecae. Begonia plebeja* and *B. sericoneura* have palmately nerved leaves with irregularly dentate to doubly dentate margins in this region and are characterized by bracteolate pistillate flowers. In its peltate leaves and whiplash trichomes, *B. fonsecae* resembles *B. conchifolia,* but differs from

this taxon in its fleshy rhizomes, larger pseudocordate leaves, ebracteolate pistillate flowers, more numerous stamens and well-developed, but unequal capsule wings. *Begonia fonsecae*'s tomentose indument immediately distinguishes it from *B. manicata* var. *peltata* which has densely squamose petioles. The only other species in Central America with peltate leaves in sect. *Gireoudia* is *B. nelumbiifolia* and these taxa differ in leaf size, peduncle length, whiplash trichome form, vestiture and sepal size. Leaves of *B. fonsecae* are smaller than those of *B. nelumbiifolia* and have correspondingly shorter petioles, significantly shorter peduncles and larger sepals. Distinctions among the peltately leaved taxa are summarized in Table 7.

24. *Begonia pinetorum* A.DC., Ann. Sci. Nat. IV. 11: 131. 1859. TYPE: MEXICO: forêts de pins, Jitotol. February 1840, *Linden 41* (Holotype: G!; isotypes: K!, P!).
Begonia tuerckheimei C.DC., Bot. Gaz. 20: 542-543. 1895. TYPE: GUATEMALA: Sesisp, 3500 ft, February 1886, *von Turckheim 885* (Holotype: US!).

Terrestrial or saxicolous herbs: *rhizomes* repent, 3-9.5 cm long; internodes very short, 0.2-0.7 (1.1) X 0.7-1.6 cm, moderately to densely tomentose when immature but glabrate with age. *Leaf blades* simple, chartaceous to subcoriaceous, oblique to transverse, asymmetric, oblong-elliptic to ovate or obovate, 6.6-16.5 (20.8) X 4.1-11 (16) cm, basally shallowly to deeply cordate, apically acute or occasionally acuminate to attenuate-acuminate, marginally obsoletely undulate to irregularly dentate-serrate, densely ciliate, sparsely to moderately tomentose above and beneath with trichomes readily rubbing off, leaving glabrous areas especially above, 8-10-palmatinerved. *Petioles* 6.8-28 cm X 2-3 (5) mm, moderately to densely tomentose, with matted trichomes 0.5-3 mm long. *Stipules* persistent, asymmetric, narrowly ovate-triangular to lanceolate, 1-2.2 X 0.7-1.4 cm, weakly keeled, apically attenuate-acuminate, marginally entire, both lamina and keel sparingly puberulous or the keel only puberulous. *Inflorescences* typically exceeding the foliage, strongly asymmetric to unilateral, densely cymose, many-flowered, 5.5-20 cm diam. *Peduncles* 26.5-74.5 cm X 3-9 mm, densely tomentose even with age, but the trichomes readily rubbing off. *Bracts* caducous, the lowermost navicular, lanceolate to narrowly ovate, 0.6-1.1 X 0.3-0.4 cm, weakly keeled, apically acuminate to attenuate-acuminate, marginally ciliate, sparsely to densely puberulous throughout. *Staminate flowers*: pedicels (2) 4-8 mm long; sepals white to pink, suborbicular to broadly ovate or obovate, (3) 4-6.5 X (3) 4-5.5 mm, glabrous to sparingly pilose; petals wanting; stamens 10-16; filaments 0.7-1.5 mm long, borne on a raised torus; anthers oblong-elliptic to obovate, 0.7-1.2 X 0.5-0.9 mm. *Pistillate flowers*: pedicels (2.5) 5-12 mm long; perianth consisting of (2) 3 or 4 subequal tepals, colored like staminate sepals, narrowly to broadly obovate, (3.5) 4.5-7 X 2.5-4 (5) mm, when 3 tepals present, the largest occasionally apically bilobed, sparsely puberulous especially basally; ovary (3) 5-9 mm long, sparsely to densely puberulous; styles 3, 1.2-1.5 mm long, connate 1/3-1/2 their length; stigmas lunate. *Capsules* with pedicels (6) 10-21 mm long, trilocular, (6) 7.5-11 mm long, puberulous; locule chambers broadly elliptic to ovate or transversely oblong-elliptic, (4) 4.5-7 X 3.5-5 (6) mm; wings 3, somewhat unequal to subequal, the largest asymmetrically ovate-triangular or oblong, (4.5) 5.5-7 (8) X (6) 7-10

(11) mm, apically obtuse to truncate, the second asymmetric, broadly oblong, ovate-triangular or lunate, 3.5-6 X (5) 7-9 mm, apically obtuse to truncate, the third equal or subequal to the second and broadly lunate to ovate-triangular or oblong.

DISTRIBUTION AND HABITAT: Southern Mexico from the states of Veracruz, Oaxaca and Chiapas to Guatemala. *Begonia pinetorum* frequently grows in damp limestone thickets and pine forests at elevations between 750-1600 m (Fig. 12).

FLOWERING: Peak flowering occurs between November and April.

DISCUSSION: *Begonia pinetorum* differs from other Central American species in the section by its pistillate flowers which regularly have three to four undifferentiated tepals. Although this trait is known in only one other species in sect. *Gireoudia*, it is widespread among other Neotropical sections. Candolle, in describing *B. pinetorum*, emphasized this character by placing it in its own section, *Psathuron* A.DC. Recognizing the similarities in other floral characters between *B. pinetorum* and sect. *Gireoudia*, Warburg (1894) and Irmscher (1925) placed *B. pinetorum* in sect. *Gireoudia*, subsection *Psathuron*. Both *B. glandulosa* Hook., as represented by plate 5256 (Smith and Schubert, 1961; Golding, 1978) and *B. nigrovenia* Regel (Golding, 1978; Smith and Wasshausen, 1983) have been treated as synonyms of *B. pinetorum*. Smith and Wasshausen (1983) have also included *B. hidalgensis* Smith & Schubert in *B. pinetorum*, stating that "material of this species ranges from the curved simple axis of typical *pinetorum* to the slightly irregular dichotomy of *hidalgensis*". Assuming that these authors are referring to inflorescence symmetry, strongly asymmetric to unilateral inflorescences are characteristic of both *B. pinetorum* and *B. hidalgensis*, but a similarity in this character is not a sound basis for synonymy in light of the differences between these taxa mentioned below. The taxa represented by these three epithets (*glandulosa, hidalgensis, nigrovenia*) can be distinguished readily from *B. pinetorum* by their glabrous upper leaf surfaces and larger capsule wings, but in salient features they are indistinguishable from one another and should be treated as *B. glandulosa* Hook. (Burt-Utley, 1984).

Begonia pinetorum is most closely related to *B. glandulosa*, with which it shares a suite of characters including its rhizomatous habit, tomentose indument, stipule form, asymmetric to unilateral inflorescences, range in stamen number, pistillate flowers with undifferentiated tepals, lunate stigmas and capsular form and pubescence. These taxa differ primarily in the previously mentioned characters and in whiplash trichome form. In *B. pinetorum* they are uniseriate basally, while in *B. glandulosa* they range from multiseriate to uniseriate basally. Ranging from central Veracruz to Guatemala, *B. pinetorum* is also more widely distributed than *B. glandulosa*, a Mexican endemic, which is known only from southeastern San Luis Potosí and northern Hidalgo.

SPECIMENS EXAMINED: MEXICO. Chiapas: W shore of Laguna Ocosingo, *Breedlove 15641* (DS, MICH, US); steep slopes adjacent to large double waterfall, 6-8 km W of Jitotol, Municipio of Jitotol, 1450 m, *Breedlove 23246* (DS, MICH, MO); 7 km NE of Bochil along rd to Simojovel, Municipio of Bochil, 1250 m, *Breedlove & Smith 32303* (DS, MEXU, MO); montane rain forest adjacent to Laguna Ocotal Grande, Municipio of Ocosingo, 800 m, *Breedlove 33092* (DS, MO); 6-10 km NNE of La Soledad along logging road from Las Margaritas to Campo Alegre, Municipio of La Independencia, 1600 m, *Breedlove 33483* (DS); Los Lagos, 3 mi NW of Rancho San José, 5000 ft, *Carlson 1721* (F); *Carlson 1859* (US); moderately dry pine forest

along gravel rd leading to Dos Lagunas, 1500 m, *Croat 46541* (MO). Oaxaca: road from Teotitlán de Camino to Chichotla, 1980 m, *Croat 48383* (MO); Jocotepec (Chinantla), *Liebmann s.n.* (B). Veracruz: limestone outcrops on hillside above San José de Gracia between Córdoba and Veracruz, 750 m, *Croat 39604* (MO). GUATEMALA. Alta Verapaz: rocky woods N of Cobán, 4300 ft, *Hunnewell 17178* (DUKE, GH); entre San Pedro Carchá y Sacoyou, 1300 m, *Molina & Molina 12051* (F, NY); Saquija, about 43 km NE of Cobán, 1200 m, *Standley 70188* (F); Finca Socuyo NE of Carchá, 1350 m, *Standley 70262* (F).

25. *Begonia dressleri* Burt-Utley, Brittonia 34: 191. 1982. TYPE: PANAMA: Colón: trail from end of Santa Rita Ridge Road to Río Piedras, 600 m, 16 February 1980. *Antonio 3762* (Holotype: MO!; isotypes: NY!, PMA!, US!). (Fig. 20).

Acaulescent herbs; *rhizomes* repent, often branching, 0.6-5.5 cm long; internodes 1-4 X 2-6 mm, sparsely villous with very narrow entire to lacerate scales 0.4-1.6 mm long. *Leaf blades* simple, membranaceous, straight or infrequently slightly oblique, asymmetrically suborbicular to broadly obovate, 1.3-4.5 X 1-4.7 cm, basally rounded to occasionally cuneate or infrequently broadly but very shallowly cordate, apically acute to acuminate, marginally ciliate, dentate to serrate at ends of major nerves and irregularly denticulate to serrulate, hirtellous to glandular-hirtellous above and beneath, 5-7-palmatinerved. *Petioles* (0.7) 1-6 (8.5) cm X 0.5-1.5 mm, sparingly to moderately hirtellous or glandular-hirtellous throughout with spreading villi 0.5-1.2 mm long. *Stipules* caducous, triangular, 1.5-5 X 2-3 mm, strongly keeled, apically acute to acuminate, marginally entire,

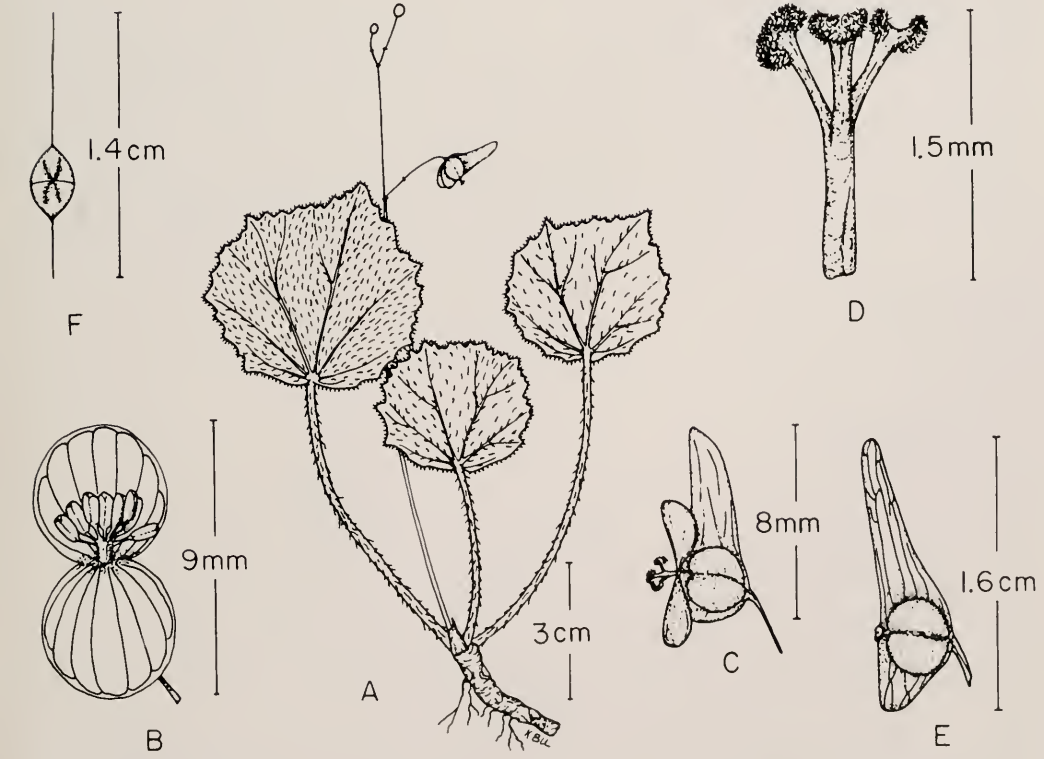

Fig. 20. *Begonia dressleri*. A. Habit. B. Staminate flower. C. Pistillate flower. D. Styles and stigmas. E. Capsule. F. Cross-section through bilocular ovary. (A-E from *Antonio 3762;* F from *Dressler 4141*).

glabrous. *Inflorescences* generally exceeding the foliage, strongly asymmetric to unilateral, laxly cymose, few-flowered, (0.5) 2-3.5 (5.5) cm diam. *Peduncles* (2.5) 4-7.5 (9.5) cm X 0.5-1 (2) mm, sparsely puberulent or glandular-puberulent. *Bracts* caducous, the lowermost navicular, triangular to narrowly triangular or lance-elliptic, 1-3 X 1-1.5 mm, apically acuminate, marginally entire to serrulate, glabrous. *Staminate flowers*: pedicels 3-9 mm long; sepals suborbicular to broadly elliptic, 3.5-4.5 (8) X 3.5-4.5 (7) mm, externally glabrous to sparingly glandular; petals wanting; stamens 7-10 (13); filaments 0.3-0.6 (1.3) mm long, borne on a raised torus; anthers oblong-obovate, 0.7-1.1 X 0.3-0.6 mm. *Pistillate flowers*: pedicels 5-8 mm long; bracteoles wanting; sepals broadly elliptic to weakly obovate, 3-4.5 X 3-3.5 mm, externally glabrous to sparingly glandular; petals wanting; ovary 3-4.5 mm long, glandular to glabrous; styles 2-3, 1-1.5 mm long, shortly branched distally, stigmas lunate. *Capsules* with pedicels 10-12 mm long, 2-3-locular, 4-5 mm long; locule chambers externally appearing cordate to transversely elliptic, 3-4 X 3-6 mm; wings 2 or 3, the largest narrowly ovate or oblong-elliptic, 8-10 X 4-5.5 mm, apically obtuse or truncate, the second asymmetrically triangular, 4.5-5.5 X 2.5-4 mm, the third subequal to the second or marginiform.

DISTRIBUTION AND HABITAT: Known only from Colón Province in Panama where it grows on moist rocks near the Río Piedras and Río Guanche between 10-600 m elevation. (Fig. 21).

FLOWERING: February-March.

DISCUSSION: Flowering when only 4 cm high, *B. dressleri* is the smallest *Begonia* known from Middle America. It is characterized by its small size, straight or rarely oblique, suborbicular to broadly obovate leaves, triangular to lance-elliptic bracts, two to three styles connate almost their entire length and capsules with long, narrow primary wings and occasionally only two wings.

In orientation and basic leaf blade form *B. dressleri* is most similar to *B. buseyi* which has straight blades with cuneate bases. These species also share similar petiolar induments composed of short villi and similar capsules with externally ovate to transversely elliptic

Fig. 21. Distribution of *Begonia buseyi* (squares) and *B. dressleri* (circles).

locule chambers and narrowly ovate to oblong primary wings. A major difference is in blade form, which is suborbicular to broadly obovate in *B. dressleri*, but narrowly elliptic, obovate to rhombic in *B. buseyi*. The upper leaf surfaces of *B. dressleri* are hirtellous to glandular-hirtellous while those of *B. buseyi* are glabrous. These species also differ subtly in stamen number which ranges from 7 to 10 (13) in *B. dressleri* and from 11 to 13 (19) in *B. buseyi*. While their capsules are similar in form, those of *B. dressleri* may be slightly larger than those of *B. buseyi* (4-5 vs 3-4 mm). (Table 11).

When pistillate flowers and capsules from the type collection were examined closely, it was found that one of the three locules frequently contained a much reduced placenta. Other collections of this species (*Dressler 4141, Mori & Kallunki 3709*) possessed unusual bilocular ovaries and capsules with either two or three stigmas and only two wings. Similar reduction in locule or wing number has not been observed in any other species in the section. Bilocular ovaries are typical of several other *Begonia* sections, including section *Weilbachia* from Middle America, but in these taxa the locules are borne laterally in the ovaries and the ovaries are three-winged. The dorsiventral locule and wing orientation observed in *B. dressleri* appears to be unique to this species.

SPECIMENS EXAMINED: PANAMA. Colón: trail from end of Santa Rita Ridge Road to Río Piedras, 1400-1600 ft, *Antonio 3903* (MO); rock face, lower Río Guanche, *Dressler 4141* (MO); Río Guanche about 2.5 km upriver from bridge on road to Portobello, 10-100 m, *Mori & Kallunki 3709* (MO).

26. *Begonia buseyi* Burt-Utley, Brittonia 34: 189. 1982. TYPE: PANAMA: Panamá: road to Cartí, San Blas, 13 km north of El Llano, 350

TABLE 11. Morphological comparison of *Begonia buseyi* and *B. dressleri*.

	B. buseyi	*B. dressleri*
Rhizome diameter (mm)	2-5	2-6
Blade orientation	straight	straight
Blade shape	elliptic, obovate or rhomboid	suborbicular to broadly obovate
Leaf blade size (cm)	3-8.5(9.7) X 1.1-2.8(5.8)	1.3-4.5 X 1-4.7
Leaf bases	cuneate	rounded to cuneate
Adaxial surface	glabrous	hirtellous to glandular-hirtellous
Primary nerves	4-5(6)	5-7
Petiole length (cm)	2.5-7.5(9.1)	(0.7)1-6(8.5)
Petiolar indument	hirtellous with villi 0.3-2 mm	hirtellous with villi 0.5-1.2 mm
Peduncle length (cm)	2.5-7.5(9.1)	(2.5)4-7.5(9.5)
Staminate sepals (mm)	3-6 X 3-6	3.5-4.5(8) X 3.5-4.5(7)
Stamens	11-13(19)	7-10(13)
Ovary length (mm)	2-3	3-4.5
Capsule length (mm)	3-4	4-5

m, 13 February 1973. *Busey 386* (Holotype: MO!; isotypes: F!, NY!, USF!). (Fig. 22).

Herbaceous perennials; *rhizomes* repent, often branching, 2.5-8 cm long; internodes 2-4 X 2.5-5.5 mm, sparsely puberulent but glabrate with age. *Leaf blades* simple, chartaceous to subcoriaceous, straight or slightly oblique, asymmetrically elliptic to obovate or rhombic,

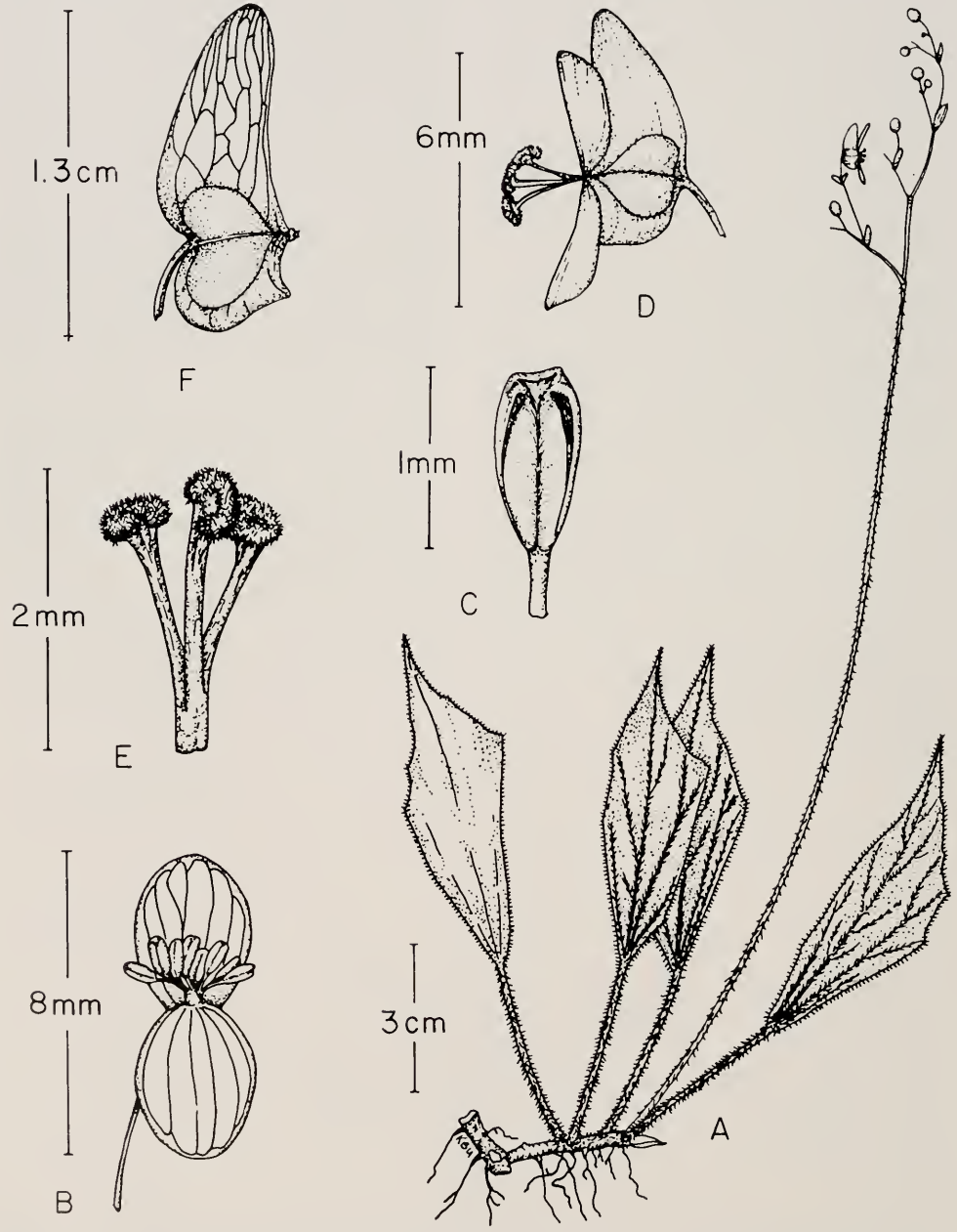

Fig. 22. *Begonia buseyi*. A. Habit. B. Staminate B. Staminate flower. C. Stamen. D. Pistillate flower. E. Styles and stigmas. F. Capsule. (from *Busey 386*).

3-8.5 (9.7) X 1.1-2.8 (5.8) cm, basally cuneate, apically attenuate-acuminate, marginally with a broad prominent lobe on one side of the midnerve, densely ciliate, obsoletely undulate, irregularly denticulate-serrulate, glabrous above and sparingly puberulent below in intercostal regions but on principal nerves moderately to densely so, 4-5 (6)-palmatinerved. *Petioles* 2.5-7.5 (9.1) cm X 0.5-1.5 mm, moderately to densely hirtellous with spreading villi 0.3-2 mm long. *Stipules* caducous, asymmetrically narrowly ovate, 5-8 X 2.5-4 mm, often strongly keeled, apically acute, marginally entire, glabrous to sparsely pilose throughout. *Inflorescences* exceeding the leaves, moderately to strongly asymmetrically cymose, few-flowered, 1.5-3 cm diam. *Peduncles* 7.3-23 cm X 0.5-2 (3) mm, sparingly glandular-hirtellous. *Bracts* caducous to subpersistent, the lowermost ovate to oblong-elliptic, 2.7-4.5 X 1.7-2.7 mm, keeled, apically rounded, marginally entire, sparingly puberulent throughout or glabrous. *Staminate flowers*: pedicels 3.7-6.5 (9) mm long, sepals suborbicular to elliptic, 3-6 X 3-6 mm, glabrous; petals wanting; stamens 11-13 (19); filaments 0.2-0.5 mm, borne on a raised torus; anthers narrowly elliptic to oblong or obovate, 0.7-1 (1.5) X (0.3) 0.5-0.7 mm. *Pistillate flowers*: pedicels 4-5 mm long; bracteoles wanting; sepals suborbicular to broadly obovate, 3-3.5 X 3-4 mm, glabrous; petals wanting; ovary 2-3 mm long, glabrous to sparingly glandular, occasionally sparsely pubescent basally; styles 3, 1.5 mm long, connate 2/3 their length; stigmas lunate. *Capsules* with pedicels 10-12 mm long; trilocular, 3-4 mm long; locules externally appearing transversely elliptic to broadly cordate, 2.5-3 X 3.5 mm, wings unequal, the largest straight to subfalcate and narrowly ovate to oblong, 9-10 X 5 mm, the second and third marginiform.

DISTRIBUTION AND HABITAT: Known only from Panamá Province in Panama where it occurs in moist areas along or near stream banks in areas E of the Canal Zone at elevations around 350 m. (Fig. 21).

DISCUSSION: *Begonia buseyi* is the only species in section *Gireoudia* with straight, narrow palmately nerved leaves that are basally cuneate and only slightly oblique apically. Such leaves are generally uncommon in *Begonia*, most species of which have oblique to transverse, basally cordate leaf blades. Along with *B. dressleri*, which it resembles in several important characters, *B. buseyi* is one of the smallest *Begonia* species in Central America. Its relationship to *B. dressleri* is discussed under this taxon. While *B. buseyi* and *B. morii* have similar petiolar induments, glabrous adaxial leaf surfaces, lunate stigmas and similar distributions in eastern Panama, the former is readily distinguished by blade characters, capsule shape and numerous morphometric differences which are summarized in Table 11.

Doubtful and Excluded Species

Begonia acutiloba Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 14. 1852. TYPE: MEXICO: Oaxaca: S. Jago Amatlán, 7/42, *Liebmann s.n.* (Lectotype: C!; isolectotypes: C!, B!).

Begonia acutiloba was included in sect. *Gireoudia* by Candolle (1864). Smith and Schubert (1946a) identified a single Guatemalan collection, *Steyermark 49379*, as *B. acutiloba* and used its pistillate flowers to characterize those of *B. acutiloba* since both pistillate and capsular material were lacking from the original Liebmann collection. This specimen differs from *B. acutiloba* in its long creeping rhizome and densely

puberulous pedicels and sepals. While appearing distinct from *B. acutiloba,* its affinities remain unknown, but it is likely an undescribed taxon in sect. *Weilbachia. Begonia acutiloba* is best considered an endemic Mexican species whose sectional alliances can not be determined unequivocally until pistillate material is available.

Begonia barsalouxii Standl. & L. Wms., Ceiba 1: 154. 1950. TYPE: HONDURAS: Dept. Olancho, trail between Catacamas and La Prensa, N of Catacamas, 500-600 m. *Standley 18540* (Holotype: US!; isotype: F, not seen).

Begonia barsalouxii, which is only known from the type collection, differs from *B. plebeja* in a number of characters including its strongly fimbriately keeled and reflexed stipules, diminutive flowers with sepals 3.5-4 x 3-3.5 mm, ebracteolate pistillate flowers and smaller capsules (6-7 mm long) with reduced dorsal wings (6-7 x 5.5-6 mm). In these characters, *B. barsalouxii* resembles *B. manicata,* with which it is apparently sympatric (*Standley 18516*). Although Standley and Williams reported that *B. barsalouxii* had an erect habit, this could not be verified from an examination of the type. In its rhizomatous habit, basally thick, broadly triangular stipules, unilateral inflorescences, serrulate and ciliate bracts and pubescence, it resembles *B. plebeja.* Eighty-two percent of the pollen from *Standley 18540* was non-staining and presumably non-viable when stained with cotton blue and lactophenol. When both its largely non-viable pollen and its characters, which are intermediate between *B. plebeja* and *B. manicata,* are considered, it seems likely that *B. barsalouxii* had a hybrid origin. Until more collections are available to permit a reevaluation of this taxon, it seems advisable to treat *B. barsalouxii* as a doubtful species.

Begonia calderonii Standl., Field Mus. Bot. 8: 27. 1930. TYPE: EL SALVADOR: Cerro de Apaneca, 1928, *Calderón 2416* (Holotype: F!).

Begonia falcata Smith and Schubert. Contrib. Gray Herb. 127: 28. 1939. TYPE: GUATEMALA: Suchitepéquez: Volcán Atitlán, south slope, 1696 m, Oct. 22, 1934, *Skutch 1485* (Holotype: GH!).

Standley's protologue and the Smith and Schubert (1961) description of this taxon do not mention locule number or sectional alliance. However, when Smith and Schubert (1939) described *B. falcata,* a synonym of *B. calderonii,* they gave its section as *Magnusia* subsection *Gireoudia* (Kl.) Irmsch. My examination of *B. calderonii* has revealed that this taxon has bilocular ovaries and a capsule form characteristic of sect. *Weilbachia.*

Begonia carpinifolia Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 20. 1852. TYPE: COSTA RICA: Candelaria, 6000 ft, *Oersted s.n.* (Holotype: C!; isotype: C!).

Gireoudia carpinifolia (Liebm.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

In his conspectus, Klotzsch (1854) transferred *B. carpinifolia* to *Gireoudia.* Recognizing floral and vegetative similarities between *B. carpinfolia* and the recently described sect. *Ruizopavonia,* Candolle (1864) included *B. carpinifolia* in sect. *Ruizopavonia.* While similar to both sect. *Gireoudia* and sect. *Ruizopavonia* in its apetalous flowers, the woody stems, pinnately nerved leaf blades and divided stigmas of *B. carpinifolia* are inconsistent with sect. *Gireoudia* and support its placement in sect. *Ruizopavonia.*

Begonia confusa Smith and Schubert, Contrib. Gray Herb. 161: 27. 1946. TYPE: GUATEMALA: creeping on rocks, Cerro Chiblac, between Finca San Rafael and Ixcán, Sierra de los Cuchumatanes, 1200-2000 m, July 22, 1942, *Steyermark 49185* (Holotype: F!; isotypes: F!, GH! [2 sheets]).

Although included in sect. *Gireoudia* (as *Magnusia*) by Smith and Schubert (1946a), habit and perianth characters of *B. confusa* more closely resemble sect. *Weilbachia*. Without critical locule information, it is impossible to accurately determine the sectional affinities of this taxon. *Begonia lindleyana* Walp., Rep. 2: 209. 1843.

Begonia vitifolia Lindl., Bot. Reg. 28. 1842. TYPE: GUATEMALA: sent to the Horticultural Society by Hartweg (Holotype: CGE!), *nom. illeg.* Art. 64.

Gireoudia lindleyana (Walp.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

Gireoudia vitifolia (Lindl.) Kl., Abh. Königl. Akad. Wiss. Berlin 207. 1855.

Using material sent by Hartweg purportedly from Guatemala, Lindley described *Begonia vitifolia* as being fruticose and having ovate leaves, but failed to mention that the leaves were also peltate. Although no mature pistillate flowers or capsules are now present on the CGE specimen, Lindley described the ovary wings as being equal and semicircular. Both Walpers (1843), when he provided a substitute name for *B. vitifolia*, and Klotzsch (1855), when he included a short description of *Gireoudia vitifolia*, repeated Lindley's original description. It seems likely that Klotzsch, in transferring *B. vitifolia* to *Gireoudia*, relied on Lindley's statement that the flowers were "dipetalous" and did not examine the specimen presently at CGE because he did not mention its peltate leaves. After examining the CGE specimen, and still without benefit of pistillate flowers, Candolle (1864) affirmed Klotzsch's evaluation of this taxon by including *B. lindleyana* in sect. *Gireoudia*, noting however that its staminate flowers occasionally had a single, obovate-oblanceolate petal and that its leaves were peltate and cordate. Citing Lindley he described the ovary as having equal wings. While peltate leaves are not uncommon in *Begonia*, the peltate, pseudocordate leaves occurring on *B. lindleyana* are very unusual. This character combination has been observed in only one other Middle American taxon, *B. fonsecae*, and a putative hybrid (*Skutch 4600*, GH) between *B. sericoneura* and *B. conchifolia*. This character combination is no more frequent in South America.

Careful examination of the CGE specimen of *B. lindleyana* revealed immature ebracteolate pistillate flowers having two sepals, apparently no petals, ovaries with equal, "semicircular" wings and four stigmas. Because of this last character, the placement of *B. lindleyana* must be reevaluated. In addition, pollen from *B. lindleyana* was unusual in consisting of predominantly malformed and presumably non-viable grains because 93.1% to 99.6% did not stain with cotton blue-lactophenol. Until further material of this taxon, which is still only known from type collected in the 1830's, is available, *B. lindleyana* must be excluded from sect. *Gireoudia* and it cannot with certainty be placed in any other section.

Begonia ludicra A.DC., Ann. Sci. Nat. IV. 11: 133. 1859. TYPE: MEXICO: Veracruz: Cordillera, swamps of Xalapa, 4000 ft, June 1840, *Galeotti 189* (Lectotype: G!; isolectotypes: BR!, K!, P!).

Weilbachia reptans Kl. & Oersted, Abh. Königl. Akad. Wiss. Berlin. 1854: 240: 1855. TYPE: MEXICO: Oaxaca: Tonaguia, 8/42, *Liebmann s.n.* (Lectotype: B!; iisolectotypes: C! [2 sheets]).

Begonia liebmannii A.DC., Prodr. 15(1): 345. Substitute name for *W. reptans* Kl. & Oersted.

When he described *B. ludicra*, Candolle (1859) included it in sect. *Gireoudia*, although he made no mention of critical stigma or ovary characters. In the Prodromus, Candolle (1864) recognized *B. liebmannii* as a distinct species in sect. *Weilbachia*. This latter species with its bilocular ovaries was subsequently synonymized with *B. ludicra* by Smith and Schubert (1961), but in their description of this taxon, they characterized the ovaries as trilocular. While I concur with their synonymy, I have observed only bilocular ovaries/capsules with two stigmas on specimens I examined and, therefore, conclude that *B. ludicra* belongs in sect. *Weilbachia*.

Begonia phyllomaniaca Mart., J. Bot. Kew Gard. Misc. 4: 206. 1852. TYPE: Hort. Bot. Monacensis? (Holotype: not seen and perhaps non-existent).

Knesebeckia phyllomaniaca (Mart.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 122. 1854.

Candolle (1864) included *B. phyllomaniaca* in sect. *Gireoudia* because of its often apetalous staminate flowers and vestiture, noting, however, that the species appeared intermediate between *B. manicata* and *B. incarnata* Link, Kl. & Otto. He also suggested that *B. phyllomaniaca* might represent either a hybrid or monstrosity. Supporting a hybrid origin for this taxon are its anthers devoid of pollen as mentioned in the protologue, morphologically intermediate characters and anatomical characters (Fellerer, 1892). Most recently, Irmscher (1960) included *B. phyllomaniaca* within sect. *Knesebeckia* as a hybrid between *B. manicata* and *B. incarnata*.

Begonia pruinata (Kl.) A.DC., Prodr. 15(1): 338. 1864.

Gireoudia pruinata Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin. 1854: 125. 1854. *nom. nud.*

Gireoudia pruinata Kl., Abh. Königl. Akad. Wiss. Berlin 1854: 207. 1855. TYPE: CENTRAL AMERICA: Grown from seed sent by Warscewicz to Berlin and cultivated by Mathieu (Holotype: B!).

Begonia pruinata is known from a single specimen at Berlin consisting of a leaf fragment and a portion of an inflorescence, and a similar specimen at Leningrad of unknown origin. Although Klotzsch (1855) included this taxon in the group within sect. *Gireoudia* with an erect habit, it is impossible to determine if this taxon is suffrutescent or rhizomatous from his description. This species has unusual ovaries with equal or somewhat subequal rounded ovary wings and also differs from most other taxa in the section by its glabrous mature petioles and leaves. More material is necessary before this species can be satisfactorily described and its affinities determined.

SPECIMENS EXAMINED: Without locality or collector (LE).

Begonia setulosa Bertoloni, Commentarii Academiae scientiarum instituti Bononiensis. Vol. 4. 437. 1840. TYPE: GUATEMALA: Volcán Agua (Holotype: presumably BOLO, not seen and perhaps non-existent).

Gireoudia setulosa (Bertol.) Kl. Abh. Königl. Akad. Wiss. Berlin. 1854: 211. 1855.

Klotzch (1855) included *B. setulosa* in *Gireoudia* based upon Bertoloni's description of this taxon which characterized the species as being caulescent, bearing both pistillate and staminate flowers with two series of two "sepals" and pistillate flowers with two stigmas. In the Prodromus, Candolle (1864) treated *B. setulosa* as a doubtful species. Without capsular or ovary characters which are lacking in Bertoloni's protologue, or critically examining Bertoloni material which could not be located in the A. Bertoloni collection at Bologna (A. Pirola, pers. comm.; Duncan, 1983), it is impossible to determine the affinities of *B. setulosa*. However, based upon the previously mentioned floral characters, it seems unlikely *B. setulosa* belongs in sect. *Gireoudia*.

Begonia stigmosa Lindl., Bot. Reg. 31: 32. 1845. TYPE: GUATEMALA: without further locality, *Hartweg s.n.* (Holotype: CGE!).

Gireoudia stigmosa (Lindl.) Kl., Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1854: 125. 1854.

In 1946 and later (1958, 1961), Smith and Schubert applied this binomial to a species occurring in Central America and northern South America which is treated herein as *B. urophylla*. Although vegetatively similar, *B. stigmosa* is distinguished readily from *B. urophylla* by its lunate stigmas and fewer stamens. The importance of these characters in delimiting *B. stigmosa* was first recognized by Irmscher (1959). With the exception of the type the only collections of *B. stigmosa* I have observed in the course of this study are from Mexico north of Chiapas, and, based on this material, *B. stigmosa* should be considered an endemic Mexican taxon.

Appendix I

Species in sect. *Gireoudia* occurring in Mexico, Central America and South America. Endemic taxa are indicated by an asterisk(*).

MEXICO

B. bettinae Ziesenhenne
B. barkeri Knowl. & Wescott
B. bowerae Ziesenhenne
B. carolineifolia Regel
B. carrieae Ziesenhenne
B. chivatoa Ziesenhenne
B. corozoensis Ziesenhenne
B. crassicaulis
B. cristobalensis Ziesenhenne
B. fusca
B. glandulosa Hook.
B. heracleifolia
B. hispidavillosa Ziesenhenne
B. hubertii Ziesenhenne
B. hydrocotylifolia Hook.
B. karwinskyana A.DC.
B. kenworthyae Ziesenhenne
B. knoopii Ziesenhenne
B. kortsae Ziesenhenne
B. manicata
B. mazae Ziesenhenne
B. multistaminea Burt-Utley
B. nelumbiifolia
B. philodendroides Ziesenhenne
B. pinetorum
B. plebeja
B. pringlei S. Wats.
B. sartorii
B. sericoneura
B. sousae Burt-Utley
B. squarrosa Liebm.
B. stigmosa
B. strigillosa

**B. tacana* Ziesenhenne
B. thiemei
**B. xilitlensis* Burt-Utley

BELIZE
B. heracleifolia
B. nelumbiifolia
B. sericoneura

GUATEMALA
B. broussonetiifolia
B. crassicaulis
B. fusca
B. heracleifolia
**B. louis-williamsii*
B. manicata
B. nelumbiifolia
B. pinetorum
B. plebeja
B. sartorii
B. sericoneura
B. strigillosa
B. thiemei
B. urophylla

HONDURAS
B. cardiocarpa
**B. fonsecae*
B. fusca
B. heracleifolia
B. manicata
B. plebeja
B. sericoneura
B. thiemei

EL SALVADOR
B. heracleifolia
B. plebeja
B. strigillosa

NICARAGUA
B. broussonetiifolia
B. cardiocarpa
B. manicata
B. multinervia
B. plebeja
B. sericoneura

COSTA RICA
B. broussonetiifolia
B. cardiocarpa
B. conchifolia
B. corredorana
B. involucrata
B. multinervia
B. nelumbiifolia
B. quaternata
B. plebeja
B. sericoneura
B. strigillosa
B. urophylla

PANAMA
**B. buseyi*
B. conchifolia
B. corredorana
**B. croatii*
**B. dressleri*
**B. garagarana*
B. heracleifolia
B. involucrata
**B. morii*
B. multinervia
B. nelumbiifolia
B. plebeja
B. quaternata
B. sericoneura
B. strigillosa
B. urophylla

COLOMBIA
B. nelumbiifolia
B. sericoneura
B. urophylla

VENEZUELA
B. urophylla

Appendix II
Key to Central American Sections of Begonia

1. Capsules dehiscing through horns or wings ..... sect. 1. *Casparya*
1. Capsules dehiscing basally along slits on sides of the wings.
   2. Staminate flowers with 2 sepals, petals generally wanting.
      3. Ovaries two-locular; capsules strongly nutant.
         4. Pistillate flowers with three stigmas .... sect. 2. *Liebmannia*
         4. Pistillate flowers with two or three stigmas .... sect. 3. *Weilbachia*
      3. Ovaries three-locular, or if 2-locular, then capsules with 2 wings; capsules inclined but not nutant.
         5. Leaves pinnately nerved, papillaceous throughout the combined stigma-style area ..... sect. 4. *Ruizopavonia*
         5. Leaves palmately nerved; papillae restricted to bands on the stigmas .... sect. 5. *Gireoudia*
   2. Staminate flowers with 2 sepals and 2 petals
      6. Placentae bipartite.
         7. Capsules bilocular, nutant .... sect. 3. *Weilbachia*
         7. Capsules trilocular, inclined to ascendant.
            8. Capsules with six wings.... ..... sect. 6. *Hexaptera*
            8. Capsules with three wings.
               9. Leaves pinnately nerved ..... sect. 7. *Podandra*
               9. Leaves palmately nerved.
                  10. Filaments free .... sect. 8. *Begonia*
                  10. Filaments monadelphous ..... sect. 9. *Knesbeckia*
      6. Placentae entire.
         11. Leaves pinnately nerved .... sect. 10. *Steineria*
         11. Leaves palmately nerved.
            12. Pistillate flowers with two perianth whorls .... sect. 11. *Urniformia*
            12. Pistillate flowers with one whorl of five tepals.
               13. Stigmatic papillae restricted to a band running the length of the stigma .... sect. 12. *Pritzelia*
               13. Stigmas papillaceous throughout.
                  14. Succulent annual herbs .... sect. 13. *Doratometra*
                  14. Suffrutescent herbs or shrubs ..... sect. 14. *Scheidweileria*

Appendix III
Synopsis of Central American Begonia Sections

The following is a synopsis of the sections which are known to occur in Central America. While no attempt has been made to evaluate the merits of these taxa, several sections are apparently of questionable merit and many are in need of revisionary study.

1. Section *Casparya* (Kl.) Warb.—1 species, *B. urticae* L.f., in Panama and Costa Rica which ranges into

South America where the section is most abundant. Most of the 31 species occur in the Andean region. The species are characterized by their unusual capsular dehiscence through the capsule horns or wings. Staminate flowers have two sepals and petals while pistillate flowers have five to six tepals. Stamens are free. Ovaries are three-locular with bipartite placentae and have three styles which are many times divided and papillaceous throughout. The species range from sufrutescent herbs to succulent herbs.

2. Sect. *Liebmannia* Ziesenhenne—perhaps 1 sp. in Central America and several in Mexico. This section, like sect. *Weilbachia,* was described to accommodate taxa with two-locular ovaries but with three styles instead of two. Both staminate and pistillate flowers have two sepals. In these and other characters this section is similar to, if not indistinguishable from sect. *Weilbachia.*
3. Sect. *Weilbachia* (Kl. & Oerst.) A.DC. —perhaps 10-15 spp. in Central America including: *B. assurgens* Irmsch., *B. calderonii* Standl., *B. carletonii* Standl. and *B. pustulata* Liebm. This section contains about 20 species and is restricted to Mexico and Central America. Species are predominantly rhizomatous. Staminate flowers have two sepals, while petals are often wanting. Pistillate flowers have two sepals, often one petal and a two-locular ovary with two or three styles. Placentae are bipartite.
4. Sect. *Ruizopavonia* A.DC.—about 7 spp. in Central America: *B. alnifolia* A.DC., *B. carpinifolia* Liebm., *B. convallariodora* C.DC., *B. cooperi* C.DC., *B. estrellensis* C.DC., *B. lignescens* Morton, *B. seemanniana* A.DC. This section of about 34 species is most abundant in the Andes. The species are characterized by their suffrutescent or shrubby habit and predominately pinnately nerved leaves. Both staminate and pistillate flowers have two sepals. Pistillate flowers have trilocular ovaries with bipartite placentae. The three styles are deeply divided and often secondarily divided, and papillaceous throughout.
5. Sect. *Gireoudia* (Kl.) A.DC.—26 spp. in Central America with another 23 endemic to Mexico. This is the best represented section in Central America. Species are primarily rhizomatous herbs, although a few taxa are suffrutescent herbs. Both staminate and pistillate flowers have two sepals and only occasionally have 1-2 petals. Ovaries are trilocular with bipartite placentae. Stigmas are bicornute to lunate, with lunate stigmas predominating.
6. Sect. *Hexaptera* Ziesenhenne—only 1 sp. in Central America, *B. oaxacana* A.DC. This taxon usually occurs in high, very wet montane habitats. Staminate flowers have two sepals and two petals while pistillate flowers have two sepals, one petal and a three locular ovary with bipartite placentae and bicornute stigmas. The most distinctive feature of this taxon is its apparent tendency to have six-winged capsules. It appears very closely related to sect. *Knesebeckia* and sect. *Begonia.*
7. Sect. *Podandra* A.DC.—possibly 1 sp. in Central America. These species have pinnately nerved leaves and staminate flowers with 2 sepals and 2 petals while the pistillate flowers have five tepals. Filaments are monadelphous. Ovaries are three-locular with bipartite placentae while stigmas are bicornuate.

8. Sect. *Begonia*—several spp. in Central America including: *B. fischeri* Schrank and *B. guaduensis* H.B.K. This section is one of the largest in the Neotropics with about 75 species, and it also occurs in the Far East. These species are herbs or suffrutescent herbs with generally palmately nerved leaves. Staminate flowers have 2 sepals and 2 petals and the filaments are free. Pistillate flowers have five to six tepals and three locular ovaries with bipartite placentae. Stigmas are bicornute. Capsular wings are unequal.
9. Sect. *Knesebeckia* (Kl.) A.D.C.—about 5 spp. in Central America: *B. biserrata* Lindl., *B. cebadillensis* Houghton ex Smith and Schubert, *B. gracilis* H.B.K., *B. ignea* (Warsz. ex Kl.) A.DC., *B. peltata* Link & Otto. There are about 37 species in the Neotropics, with a concentration in Mexico, but the section is also poorly represented in the Far East. Species in this section appear similar to those in sect. *Begonia* in plant habit but have staminate flowers with monadelphous filaments. With the inclusion of sect. *Rachia* (Irmscher, 1960), species in this section have pistillate flowers with four to five tepals or two sepals and a petal. Stigmas are bicornute to lunate.
10. Sect. *Steineria* (Kl.) A.DC.—In Central America this section is represented only by *B. opuliflora* Putz. from Panama. Although included in the Flora of Panama (Smith and Schubert, 1958), no collections have been seen from there. The remaining five species are primarily Brazilian. Species in the section are shrubby with pinnately veined leaves. Staminate flowers have two sepals and two petals and stamens with free filaments; pistillate flowers have five tepals, three-locular ovaries, entire placentae and bicornute stigmas that are papillaceous throughout.
11. Sect. *Urniformia* Ziesenhenne—1 species in Central America. *Begonia heydei*, the only known species, is a small, succulent, perennial herb that is often deciduous during the dry season. Staminate flowers have two sepals and two petals, while the stamens may be monadelphous. Pistillate flowers have two sepals, a petal and a unilocular ovary with entire placentae and somewhat bicornute stigmas. The most distinctive characteristics of this taxon are the apparently unilocular ovaries and unusual elongate, hollow wings on the capsules.
12. Sect. *Pritzelia* (Kl.) A.DC.—1 species in Central America: *B. glabra* Aubl. This is one of the largest sections with almost 100 species that are primarily South American. Staminate flowers have two sepals and two petals while pistillate flowers are characterized by five tepals, entire placentae, three-locular ovaries, bicornute stigmas that are papillaceous throughout and unequal capsule wings.
13. Sect. *Doratometra* (Kl.) A.DC.—About 4 spp. in Central America: *B. wallichiana* Lehmann, *B. hirsuta* Aubl., *B. semiovata* Liebm. and *B. tonduzii* C.DC. The section contains about 12 species, all of which are most abundant in lowland tropical environments. They have very succulent stems and are predominantly annuals. Staminate flowers consist of two sepals and sometimes two petals and free or monadelphous filaments. Pistillate flowers are characterized by four or five tepals, three-locular ovaries with entire placentae and bicornute stigmas.

14. Sect. *Scheidweileria* (Kl.) A.DC.—A South American section of about six species, of which only *B. parviflora* Poepp. and Endl. extends into southern Central America. The species are shrubby with palmately lobed leaves and small flowers. Staminate flowers have two sepals, two petals and free filaments. Pistillate flowers have five tepals, three-locular ovaries with entire placentae and bicornute stigmas that are papillaceous throughout.

Acknowledgments

This paper is based in part upon a doctoral dissertation submitted to the Department of Botany, Duke University, Durham, North Carolina. I am indebted to Dr. Robert L. Wilbur for his assistance, direction, encouragement and patience throughout the course of this research. I also wish to thank the members of the Botany Department at Duke, especially Dr. William C. Culberson and members of my committee: Dr. Louis E. Anderson, Dr. Aubrey W. Naylor, Dr. Donald E. Stone and Dr. J. Bolling Sullivan from the Duke Marine Laboratory for their support. Field research was supported in part by National Science Foundation Grant No. DEB-76-10185 to Dr. Robert L. Wilbur. Travel to work at MEXU was supported by an award from the Herbario Nacional, Instituto de Biologia, Universidad Autonoma de Mexico. Much of the research involved in this study was conducted during a year and a half's residence at the U. S. National Herbarium. I wish to express my gratitude to Dr. Lyman B. Smith who welcomed the prospect of my working with *Begonia* and was a source of advice and encouragement during my stay at the Smithsonian. I also wish to thank Janet Forbes for her typing of the present manuscript. Many other individuals have contributed to the success of the present study and I wish to thank them: Dr. Frank Almeda, Richard Baker, Dr. William Burger, Dr. Thomas Croat, Ellen Farr, Luis Diego Gomez, Sherri Herndon, Marie Le Blanc, Ronald Liesner, Dr. James Luteyn, Dr. Dan Nicolson, Dr. Harold Robinson, Dr. M. J. Sands, Ruth Shallart, Dr. Mario Sousa and my colleagues at the University of New Orleans. I also wish to express my gratitude to my husband, Dr. John F. Utley for his support and assistance during this study.

I am grateful to the curators of the following herbaria who loaned specimens and made their facilities available for study. Arnold Arboretum, Harvard University (A); Botanisches Museum Berlin-Dahlem (B); L. H. Bailey Hortorium, Cornell University, Ithaca (BH); British Museum (Natural History), London (BM); Jardin Botanique del État, Bruxelles (BR); Botanical Museum and Herbarium, Copenhagen (C); California Academy of Sciences, San Francisco (CAS); University of Cambridge (CGE); Muséo Nacional de Costa Rica, San Jose (CR); Dudley Herbarium, Stanford University (DS); Duke University, Durham (DUKE); Field Museum of Natural History, Chicago (F); Conservatoire et Jardin Botanique, Genève (G); Herbarium van de Rijksuniversiteit, Gent (GENT); Gray Herbarium, Harvard University (GH); Botanische Anstalten der Martin-Luther Universität, Halle (HAL); Institut fur Allgemeine Botanik und Botanischer Garten, Hamburg (HBG); Royal Botanic Gardens, Kew, England (K); V. L. Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad (LE); Herbarium et Jardin de l'Université, Liège (LG); Lundell Herbarium, Austin (LL); Botanische Staatssammlung, Mü-

nchen (M); Herbario Nacional, Instituto de Biología, Universidad Nacional Autónoma de México, D.F. (MEXU); University of Michigan, Ann Arbor (MICH), Missouri Botanical Garden, St. Louis (MO); Michigan State University, East Lansing (MSC); New York Botanical Garden, Bronx (NY); Muséum National d'Histoire Naturelle, Paris (P); University of Texas, Austin (TEX); University of California, Berkeley (UC); University of California, Riverside (UCR); United States National Herbarium, Washington, D.C. (US); University of South Florida, Tampa (USF); University of Vermont, Burlington (VT); Naturhistorisches Museum, Wien (W); University of Wisconsin, Madison (WIS).

Resumen

Begonia sect. *Gireoudia* es la mas grande de 14 secciones de *Begonia* que ocurren en America Central. Este es un grupo relacionado fenéticamente que se puede diferenciar de otras secciones por la morfologia floral agregado al hábito de plantas. De las 26 especies reconocidas aqui de America Central, 16 de ellas son endemicas a la región, mas bien en Costa Rica y Panamá donde se encuentran desde al nivel del mar hasta a mas de 2,000 m de altura. La necesidad de hacer un estudio sistemático intenso se notó cuando se trató de identificar especies de la parte sur de América Central con los tratamientos florísticos posibles.

Durante la última parte de 3 años residiendo en Costa Rica, con subsecuentes viajes a Costa Rica y Panamá, y trabajo hecho recientemente en México, especies con sect. *Gireoudia* se recogieron intensamente y se hicieron observaciones del campo. Todo ésto mas informacion combinadas con mas de 3,000 ejemplares del herbario, ha permitido una revaluación de especies dentro la sect. *Gireoudia*. Cinco species nuevas fueron descubiertas entre las 26 especies en sect. *Gireoudia* que se encuentran en America Central; cuatro fueron panameñas y una guatemalteca. Como resultado de estos estudios, taxas recogidas mas sequido, *B. sericoneura,* y *B. urophylla* se han vuelto a interpretar, mientras tanto, otras dos especies *B. broussonetiifolia* y *B. cardiocarpa* que en floras recientes se habian encontrado en sinonomía, ahora se reconocen que son distintas. Con este nuevo modo de tratar estas especies, se discuten los importantes caracteres morfológicos par distinguir las especies en sect. *Gireoudia* junto con los mayores caracteres florales y vegetativos. Una clave detallada para las secciones de especies de America Central están incluidas. Cada especie lleva una descripción completa de los detalles morfológicos junto con una discusión de la afinidad con otra taxa en la sección de America Central. Se prepararon tablas para comparar fenéticamente la taxa similar y distribución de mapas se han incluido para todas las especies. Las especies recientemente descritas han sido ilustradas con dibujos de líneas. Las especies fueron divididas en 13 grupos de especies basado en la similaridad morfológica entre la taxa.

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ISSN 0082-6782

TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 25, Number 2 $5.50 November 3, 198

SYSTEMATICS OF THE KEY SILVERSIDE, MENIDIA CONCHORUM, WITH COMMENTS ON OTHER MENIDIA SPECIES

CHARLES F. DUGGINS JR., ALVAN A. KARLIN, KENNETH RELYEA AND RALPH W. YERGER p. 133

GEOGRAPHIC VARIATIONS IN GULF SLOPE POPULATIONS OF THE BLUNTNOSE DARTER, ETHEOSTOMA CHLOROSOMUM (HAY)

HENRY L. BART, JR., AND ROBERT C. CASHNER p. 151

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Volume 25, $8.50 domestic, $9.50 foreign

Copies of *Tulane Studies in Zoology and Botany* sent to regular recipients, if lost in the mails, will be replaced if the editorial offices are notified before the second subsequent issue is released.

COMMUNICATIONS: Address all queries and orders to: Editor, TSZ&B, Department of Biology, Tulane University, New Orleans, Louisiana 70118, U.S.A.
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PRINTED BY E. O. PAINTER PRINTING COMPANY, P. O. BOX 877, DELEON SPRINGS, FLORIDA 32028.

TULANE STUDIES IN ZOOLOGY AND BOTANY

Volume 25, Number 2 $5.50 November 3, 1986

Systematics of the Key Silverside, *Menidia conchorum*, with Comments on other *Menidia* species (Pisces: Atherinidae)

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Abstract

Populations of *Menidia conchorum* are electrophoretically and meristically compared to *M. beryllina, M. peninsulae* and *M. colei*. The ecological status of *M. conchorum* is also discussed.

Meristically, *Menidia conchorum* and *M. peninsulae* differ to an extent that could by traditional taxonomic analysis be considered distinct species. Electrophoretically, *M. conchorum* does differ from *M. beryllina* and *M. colei*, but not from *M. peninsulae*. We feel that in *Menidia*, the electrophoretic data are more reliable than the meristic data because of environmental influences on meristics. Therefore, we conclude that *M. conchorum* and *M. peninsulae* are conspecific. The name *Menidia peninsulae* has nomenclatural priority. Johnson's (1975) distinction between *M. beryllina* and *M. peninsulae* is also supported.

Introduction

The genus *Menidia* as currently recognized contains eight or nine species (Robbins, 1969; Johnson, 1975; Echelle and Mosier, 1981,1982; Chernoff et al., 1981): *Menidia menidia* (L) from Newfoundland to northeastern Florida; *M. beryllina* (Cope) from Massachusetts to Vera Cruz, Mexico; *M. audens* Hay, Mississippi Valley, considered conspecific with *M. beryllina* by Chernoff et al. (1981); *M. extensa* Hubbs and Raney, restricted to Lake Waccamaw, North Carolina; *M. peninsulae* (Goode and Bean), Atlantic coast from northeastern Florida to Ft. Pierce, Florida, and on the Gulf of Mexico coast from Marco Island, Florida to near Brownsville, Texas (eastern and western Gulf populations may be allopatric, Chernoff et al., 1981); *M. clarkhubbsi* Echelle and Mosier, an all female species from the Texas Gulf coast; *M. conchorum* Hildebrand and Ginsburg, Florida Keys; and *M. colei* Hubbs, Yucatan, Mexico.

Menidia colei was placed with *M. conchorum* in a new genus, *Menidiella*, by Schultz (1948). This action has not been generally followed. Miller (1966, 1976) allocated *M. colei* and *M. conchorum* to the genus *Menidia* even though no data were presented, nor other studies cited, to support such a decision. We follow Miller (1966,1976), although we feel that a critical generic level study is in order. Since *M. colei* and *M. conchorum* were originally considered by Schultz

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(1948) to be closely related, we include an examination of the relationships of the two forms in this paper, in addition to comparisions of *M. conchorum* to *M. beryllina* and *M. peninsulae*. We do not treat further the generic level taxonomic problem.

The Key Silverside, *Menidia conchorum* Hildebrand and Ginsburg (1927), is distinguished from other *Menidia* by its low anal fin ray number compared to all species except *M. colei* and by its small size. Gilbert (1978) noted that the Key Silverside could also be distinguished by its lower number of lateral and predorsal scales. Only *M. colei* has lower numbers for these traits (Tables 2-5). Air bladder morphology has been used to distinguish *M. beryllina* from *M. peninsulae* (Echelle and Mosier, 1981), and *M. conchorum* resembles *M. peninsulae* in this trait. However, use of this trait for identification has been controversial and we refer the reader to Echelle and Mosier (1981, 1982), Edwards et al. (1978) and Chernoff et al. (1981). We feel that the trait can be used for field identification, and thus follow Echelle and Mosier (1981). In addition, Chernoff et al. (1981) showed that in *M. peninsulae* the anal fin originates under the last precaudal or first caudal vertebra, while in *M. beryllina* it originates one or two vertebrae farther forward. *Menidia conchorum* again resembles *M. peninsulae* in this characteristic.

Based on its limited geographic distribution in the lower Florida Keys, *M. conchorum* was designated as an endangered species (Gilbert, 1978). Continued investigation has resulted in the gradual extension of the known range of *M. conchorum*. Hildebrand and Ginsburg (1927) and Robbins (1969) reported *M. conchorum* only from Boca Chica (near Key West in the lower Florida Keys). One of us (KR) collected the species at Big Pine Key in 1965. Johnson (1975) and Miller (1976) considered *M. conchorum* a rare species, but Gilbert (1978) reported Key Silversides to be wide-spread in the lower Florida Keys. Field collections for the present study revealed seemingly large populations of *M. conchorum* in the middle Florida Keys (Long and Grassy Keys) as well, narrowing the gap in the presumed allopatric distribution of *M. conchorum* with respect to congeners *M. beryllina* and *M. peninsulae*.

In the present study, we define the relationships of the nominal *M. conchorum* by use of both morphological and biochemical characters to other *Menidia* species, and examine variation within the nominal *M. conchorum*. This has necessitated examination of meristic, morphometric and electrophoretic traits for *M. conchorum, M. peninsulae. M. colei, M. beryllina* and *M. menidia*. The latter is only marginally treated as it is quite distinct and geographically far removed from *M. conchorum*. The lacustrine *M. extensa* and the nominal *M. audens* are not considered. *Menidia clarkhubbsi*, of presumed hybrid origin (see Echelle and Mosier, 1981, 1982) is likewise not considered. We include biochemical data for *M. colei* only for comparative purposes to *M. conchorum*, not for analysis in itself, as Echelle will report more extensive data for that species.

Materials and Methods

Materials.—Between June, 1977 and December, 1979, 840 individuals from 21 localities (see locality data and Figure 1) were collected. Collections of *Menidia* were made with a seine or by dipnetting from a shallow draft boat at night. *Menidia* species were separated by taxon when more than one taxon occurred at a locality, and then each species collec-

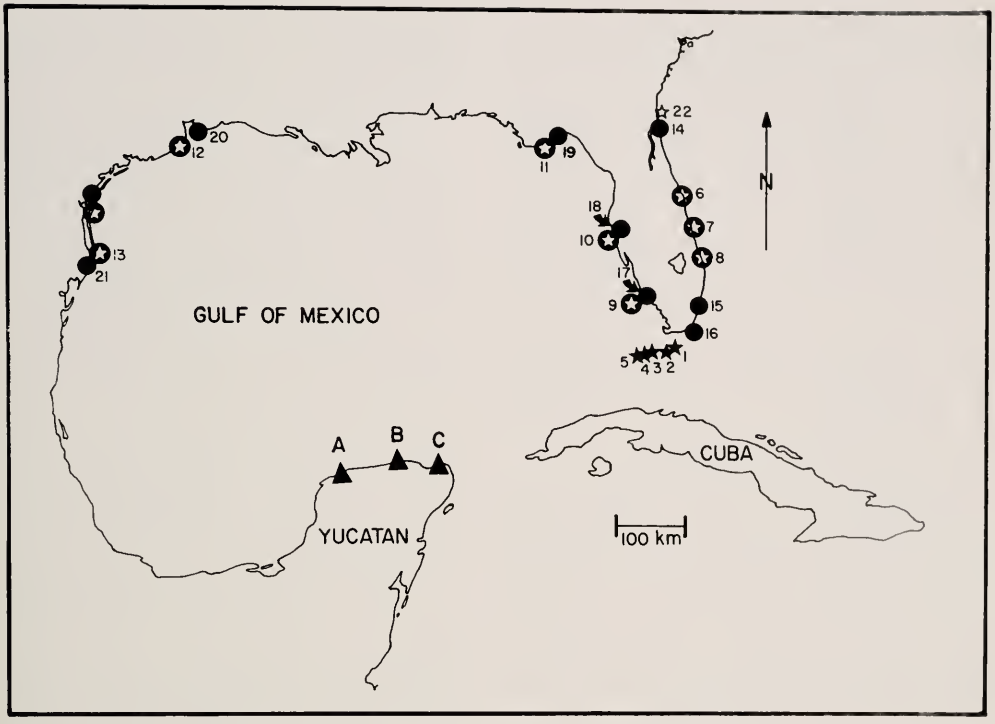

Fig. 1. Collection localities. Numbers and letters refer to populations used for electrophoresis (see Methods and Materials). Symbols: ● = *M. beryllina*, ▲ = *M. colei*, ★ = *M. conchorum*, ✪ = *M. peninsulae*, ☆ = *M. menidia*.

tion was subdivided into two groups of at least 20 individuals per group. One sub-group was preserved in 10% buffered formalin and used for morphological analysis. The other subgroup was placed in a plastic bag, covered with the water in which it was collected, and placed on a block of dry ice until returned to the laboratory. Once in the laboratory, the preserved specimens were washed overnight with tap water and transferred to 40% isopropanol, and the frozen specimens were stored at –70° C until used for electrophoresis.

LOCALITIES.—*Menidia conchorum:* Florida, Monroe County: population number 1) Long Key (20 specimens for electrophoresis; 40 specimens for morphological analysis); 2) Grassy Key (20;24); 3) Big Pine Key (20;30), 4) Cudjoe Key (20;26), and 5) Rockland Key (20;29).

Menidia peninsulae: Florida: 6) Brevard Co., Indian River near Titusville (20;30); 7) Brevard Co., Sebastian Inlet (20;35); 8) St. Lucie Co., Indian River at Ft. Pierce (20;41); 9) Collier Co., Tigertail Beach, Marco Island (20;30); 10) Hillsborough Co., Anna Maria Beach, Tampa Bay (20;30); and 11) Wakulla Co., St. Marks Lighthouse (20;30). Texas: 12) Galveston Co., San Luis Pass (20;30), 13) Cameron Co., Brownsville (20;30), and one additional population not used for electrophoresis from Aransas Co., Corpus Christi beach at Rockport (30).

Menidia beryllina: Florida: 14) Duval Co., Jacksonville (20;30), 15) Broward Co., Deerfield Beach (20;24); 16) Monroe Co., Key Largo (20;35); 17) Collier

Co., 2 km north of Marco Island (20;30); 18) Hillsborough Co., Alafia River at Federal Highway 41, Tampa Bay (20;26); and 19) Wakulla Co., St. Marks Lighthouse (20;30). Texas: 20) Chambers Co., Gilchrist Inlet (20;30); 21) Galveston Co., San Luis Pass (20;30); and two localities not used for electrophoresis, one from Florida, Dade Co., Miami, pond at University of Miami (29) and one from Texas, Nueces Co., Corpus Christi, Mustang Island State Park (30).

Menidia menidia: 22) Florida, Duval Co., St. Johns River (20;30).

Menidia colei: Mexico: A) 2.1 km south of Progreso (20;35); B) Rio Lagartos, beach on west side of city (20;35); and C) State of Quintana Roo, Chiquila (20;40).

Morphological Methods.— Counts and measurements, taken from the left side of the body, followed Hubbs and Lagler (1958). Measurements from adult specimens (greater than 35mm SL) were recorded to the nearest 0.1mm with dial calipers and were converted to a percentage of standard length. Measurements are not reported as none, in our opinion, provided significant data, but are available in Duggins, 1980 (unpublished Ph.D. dissertation, Florida State University) or from the senior author upon request. Four meristic characters were of interest in this study: number of anal fin rays, predorsal scales, lateral scales, and vertebrae (recorded from radiographs). Other traits did not yield significant results and are not reported. These data are also available from the senior author upon request.

Meristic data were analyzed by comparision of mean values by a t-test with significant level set at $p<0.01$.

Specimens used for morphological analysis were deposited in the Ichthyological collection at Florida State University, now housed at the Florida State Museum, Gainesville.

Electrophoretic Methods.— To obtain protein samples for electrophoresis, entire individuals were homogenized in an equal volume of chilled distilled water; the slurry that resulted was centrifuged at 25,000g at 4° C for 60 min. The supernatant of water soluble proteins was decanted and stored at 4° C overnight, a maximum of 18 hours prior to electrophoretic separations. At the conclusion of the study, individual tissues (liver, muscle, eye) were subjected to electrophoretic separations to ascertain the source of each isozyme (Table 1).

Table 1 lists the 27 loci coding for proteins surveyed in this study. Techniques of starch gel electrophoresis were similar to those described by Brewer (1970) and Selander et al. (1971) with the following modifications: Gp, Est, Gpi, and Ldh were resolved on the LiOH discontinuous ion system described by Selander et al. (1971) and Adh, GA-3-pdh, Sod, Ak, G-3-pdh, Gldh, Icdh, Mdh, Pgdh, Pgm and Xdh were surveyed on the tris-citrate-EDTA pH 7.1 ion system described by Ayala et al. (1972). Staining for Gldh was modified from Buth and Berg (1979) to contain 9.0g D-glucose, 0.005g each of NBT, MTT, PMS and 0.01g of NADP. All gels were 12.5% starch (Electrostarch, Lot 307, Otto Hiller Electrostarch Co., Madison, Wisconsin).

The locus nomenclature system follows Fisher et al. (1980) and Crabtree and Buth (1981). When electromorph (allelic) variation occurred, the electromorph with the greatest anodal migration was called *a*, the next *b*, and so on.

Electrophoretic data were summarized with Nei's (1972) standard genetic distance statistic, D. Average

TABLE 1. Enzymes systems surveyed in this study.

Enzyme	Locus	Tissue examined
Alcohol dehydrogenase	Adh	liver
Adenylate kinase	Ak	muscle
Esterase	Est-1,2	liver/muscle
Glucose dehydrogenase	Gldh	liver
Glucosephosphate isomerase	Gpi-A	muscle
	Gpi-B	muscle
Glyceraldehyde-3-phosphate dehydrogenase	GA-3-pdh-A	muscle
	GA-3-pdh-C	liver
alpha-Glycerophosphate dehydrogenase	G-3-pdh-B	liver
Isocitrate dehydrogenase	M-Icdh-A	muscle
	S-Icdh-A	liver
Lactate dehydrogenase	Ldh-A	muscle
	Ldh-B	muscle
	Ldh-C	eye
Malate dehydrogenase (NAD-dependent)	S-Mdh-A,B	eye/liver/muscle
Non-enzymatic proteins	Gp-1,2,3,4	liver/muscle
Superoxide dismutase	Sod	liver
Phosphoglucomutase	Pgm-A,B	muscle
Phosphogluconate dehydrogenase	Pgdh-A	muscle
Xanthine dehydrogenase	Xdh-A	liver
	Xdh-B	muscle

genetic distances ($\bar{D}$) and standard deviations were derived from the standard genetic distance matrix as the arithmetic means and the standard deviations about those means.

Status

Menidia conchorum is an elusive fish, thus collections of this fish have been few. The species is, however, common and found in protected mangrove bordered coves of the lower Florida Keys, notably Rockland, Cudjoe and Big Pine Keys. We feel that further sampling would show that it occurs throughout the lower Florida Keys. In our fieldwork we also found large populations in the middle Florida Keys (Grassy and Long Keys), in ecological conditions similar to those of the lower Florida Keys. The species forms fast moving schools during the day. This plus the soft coralline marl substrate make them difficult to seine. The Key Silverside is much more easily caught by dipnet at night from a shallow draft boat, a method that was successful for us.

It is probable that much habitat suitable for *M. conchorum* has been destroyed by road construction and commercial development, especially in the upper Florida Keys and around Key West. Of note is that Fowler (1945) reported *Menidia* (possibly *M. conchorum*) from Big (Upper) Matecumbe Key, but Robbins (1969) was unable to confirm that record. Fowler (1945) clearly delineated between *Menidia* and *Atherinomorus* (the Hardhead Silverside) in his monograph, and we have no reason to doubt the validity of the Big Matecumbe record of *Menidia*. This Key is only a few kilometers up the Florida Keys from Long Key, the current northernmost Key known to have a population of *M. conchorum*. The species may still exist at upper Matecumbe Key, or it could have been extirpated. It is also possible that Fowler's (1945) record could have been *M. beryllina*, which we have collected still farther north (Key

Largo), but not as far southward in the Florida Keys as Big Matecumbe.

It is unlikely that *M. conchorum* is restricted to the Florida Keys contacted by Federal Highway 1; there are probably populations on outlying Florida Keys. Although individual Key Silverside populations are seemingly large, we would caution that these populations should still be considered endangered, even though we believe that Florida Keys populations represent southernmost *M. peninsulae* (see conclusions).

Analysis of Meristic Variation

Four meristic traits are reported in the present paper (Tables 2-5). Within the Tables, populations of each species are grouped, and within a species the populations are reported from north to south on the Florida east coast and in the Florida Keys; thence around the Gulf of Mexico from east to west and into Yucatan (see Figure 1). The Tables indicate statistically significant ($p<0.01$) differences between mean values of geographically adjacent populations. Important statistically significant mean values not indicated in the Tables are: anal fin rays—1) Long Key *M. conchorum* vs. Marco Island *M. peninsulae* and Marco Island *M. beryllina;* Long Key *M. conchorum* vs. Key Largo *M. beryllina* 2) Marco Island *M. peninsulae* vs. Ft. Pierce *M. peninsulae;* Marco Island *M. peninsulae* vs. Marco Island *M. beryllina* 3) Marco Island *M. beryllina* vs. Key Largo *M. beryllina* 4) *M. colei* vs. Florida Keys *M. conchorum* and Brownsville populations of *M. beryllina* and *M. peninsulae.* Predorsal scales—1) Long Key *M. conchorum* vs. Marco Island *M. beryllina* 2) Marco Island *M. beryllina* vs. both Key Largo *M. beryllina* and Marco Island *M. peninsulae* 3) *M. colei* vs. Florida Keys *M. conchorum* and Brownsville populations of both *M. beryllina* and *M. peninsulae.* Lateral scales—1) Long Key *M. conchorum* vs. Marco Island *M. peninsulae,* Marco Island *M. beryllina* and Key Largo *M. beryllina* 2) Marco Island *M. peninsulae* vs. both Ft. Pierce *M. peninsulae* and Marco Island *M. beryllina* 3) Marco Island *M. beryllina* vs. Key Largo *M. beryllina* 4) *M. colei* vs. Florida Keys *M. conchorum* and Brownsville populations of both *M. peninsulae* and *M. beryllina.* Vertebral number 1) Long Key *M. conchorum* vs. Marco Island populations of both *M. beryllina* and *M. peninsulae* 2) Marco Island *M. beryllina* vs. Marco Island *M. peninsulae* and Key Largo *M. beryllina* 3) *M. colei* vs. Florida Keys *M. conchorum* and Brownsville populations of *M. beryllina* and *M. peninsulae.*

Meristic traits in *Menidia* are exceedingly difficult to analyze. Within a given species, some populations can be more different from other populations than they are from nearby or sympatric populations of a different species. For example, for the four meristic traits presented here (Tables 2-5), Key Largo *M. beryllina* are quite different from all other *M. beryllina.* However, they also differ from *M. peninsulae,* and are electrophoretically clearly *M. beryllina.* They are, however, more similar to adjacent *M. conchorum* in meristic traits, but not electrophoretically. Similarly, the Rio Lagartos population of *M. colei* is markedly different for the four meristic features from other *M. colei* populations, but does not differ electrophoretically. In *Menidia,* there is little intraspecific electrophoretic variation, but there is marked intraspecific meristic variation, either clinally or within a local population for no evident reason.

Analysis is presented here as variation within a species and then by a species to species comparision, followed by a summary.

TABLE 2. Number of anal fin rays in *Menidia* populations. An asterisk or an x next to consecutive populations indicates statistically significant ($p<0.01$) difference between mean values. Other such differences are indicated in the text.

Population	9	10	11	12	13	14	15	16	17	18	19	20	N	$\bar{X}$	s
beryllina-Atlantic (Florida)															
Jacksonville							5	12	12	1			30	16.3	0.8
Deerfield							3	10	7	3	1		24	16.5	1.0
Miami								7	10	8	4		29	17.3	1.0*
Key Largo						8	18	9					35	15.0	0.7*
peninsulae-Atlantic (Florida)															
Titusville						3	15	11	1				30	15.3	0.7
Sebastian Inlet						3	10	9	12	1			35	15.9	1.1
Fort Pierce						8	11	16	6				41	15.5	1.0*
conchorum-Florida Keys															
Long Key					9	24	6	1					40	13.9	0.7*
Grassy Key					11	11	2						24	13.6	0.7x
Big Pine Key				8	13	8	1						30	13.1	0.8x
Cudjoe Key				5	14	7							26	13.1	0.7
Rockland Key				8	15	5	1						29	12.9	0.8
TOTAL				21	62	55	10	1					148	13.4	0.7
peninsulae-Gulf of Mexico															
Marco Island (Florida)					2	12	12	6					30	14.7	0.9
Tampa (Florida)						10	7	10	3				30	15.2	1.0
St. Marks (Florida)						2	9	12	7				30	15.8	0.9*
San Luis Pass (Texas)							5	2	10	10	1	1	29	17.2	1.4*
Rockport (Texas)							3	9	10	5	3		30	16.9	1.1
Brownsville (Texas)							4	13	10	2	1		30	16.4	0.9
beryllina-Gulf of Mexico															
Marco Island (Florida)						1	6	14	7	2			30	16.1	0.9
Tampa (Florida)						1	2	12	10	1			26	16.3	0.8
St. Marks (Florida)						1	7	14	5	2	1		30	16.1	1.1*
Gilchrist (Texas)								12	11	6	1		30	16.9	0.9*
Corpus Christi (Texas)								14	13	11	3		30	16.6	0.7
Brownsville (Texas)							1	6	14	6	2	1	30	17.2	1.1
colei-Yucatan															
Progreso	1	12	22	5									40	10.8	0.7*
Rio Lagartos			8	20	12								40	12.1	0.7*x
Chiquila	3	14	19	2									38	10.5	0.7x
TOTAL	4	26	49	27	12								118	11.1	1.0

TABLE 3. Number of predorsal scales in *Menidia* populations. An asterisk or an x next to consecutive populations indicates statistically significant ($p<0.01$) difference between mean values. Other such differences are indicated in the text.

Population	9	10	11	12	13	14	15	16	17	18	19	N	$\bar{X}$	s
beryllina-Atlantic (Florida)														
Jacksonville									22	7	1	30	17.3	0.5*
Deerfield						1	7	14	3			25	15.7	0.7*
Miami							8	13	4			25	15.8	0.7x
Key Largo					2	10	16	6				34	14.8	0.8x
peninsulae-Atlantic (Florida)														
Titusville						11	11	8				35	14.9	0.8
Sebastian Inlet						8	24	4				35	14.9	0.6
Fort Pierce					2	16	18	3	1			40	14.6	0.8
conchorum-Florida Keys														
Long Key					3	18	12	5				38	14.5	0.8*
Grassy Key					7	13	5					25	13.9	0.7*x
Big Pine Key				1	19	10						30	13.3	0.5x
Rockland Key				8	12	7	2					29	13.1	0.9
TOTAL				9	41	48	19	5				122	14.0	0.9
peninsulae-Gulf of Mexico														
Marco Island (Florida)						10	11	5				26	14.8	0.7
Tampa (Florida)						7	16	3				26	14.9	0.6
St. Marks (Florida)						3	19	7	1			30	15.2	0.7*
San Luis Pass (Texas)						1	7	17	4	1		30	15.9	0.8*
Rockport (Texas)						1	8	16	5			30	15.8	0.8
Brownsville (Texas)						1	8	13	7			29	15.9	0.8
beryllina-Gulf of Mexico														
Marco Island (Florida)							5	14	8	2		29	16.2	0.8*
Tampa (Florida)					1	1	4	17	4			27	15.8	0.9*x
St. Marks (Florida)							4	12	13	1		30	16.4	0.8x
Gilchrist (Texas)							4	13	11	2		30	16.4	0.8*
Corpus Christi (Texas)							15	10	5			30	15.7	0.8*
Brownsville (Texas)						1	16	7	4	1	1	30	15.7	1.1
colei-Yucatan														
Progreso	2	26	8	3								39	10.3	0.7*
Rio Lagartos		10	17	10	2							39	11.1	0.9*
Chiquila	1	14	18	5								38	10.7	0.7
TOTAL	3	50	43	18	2							116	10.7	0.7

TABLE 4. Number of lateral scales in *Menidia* populations. An asterisk or an x or y next to consecutive populations indicates statistically significant ($p<0.01$) difference between mean values. Other such differences are indicated in the text.

Population	28	29	30	31	32	33	34	35	36	37	38	39	40	41	N	$\bar{X}$	s
beryllina-Atlantic (Florida)																	
Jacksonville										4	8	12	5	1	30	38.7	1.0*
Deerfield								5	8	8	4				25	36.4	1.0*x
Miami									2	12	16	1			31	37.3	0.7xy
Key Largo						2	13	15	3						33	34.6	0.8y
peninsulae-Atlantic (Florida)																	
Titusville									4	10	11	4			29	37.5	0.9
Sebastian Inlet									1	12	13	8	1		35	37.9	0.9*
Fort Pierce									5	28	5	3			41	37.2	0.7*x
conchorum-Florida Keys																	
Long Key							4	18	12	3					37	35.4	0.8x
Grassy Key							5	15	4	1					25	35.0	0.7
Big Pine Key						2	10	14	3						29	34.6	0.8*
Cudjoe Key						10	10	5							25	33.8	0.8*
Rockland Key						5	17	4	1						27	34.0	0.7
TOTAL						17	46	56	20	4					143	34.6	0.9
peninsulae-Gulf of Mexico																	
Marco Island (Florida)									1	7	18	3			29	37.8	0.7*
Tampa (Florida)										1	12	9	3		28	38.4	0.9*
St. Marks (Florida)											9	15	3	1	28	38.9	0.8x
San Luis Pass (Texas)										6	14	7	2		29	38.2	0.9x
Rockport (Texas)										6	15	8			29	38.1	0.7*
Brownsville (Texas)									3	10	15	2			30	37.5	0.8*
beryllina-Gulf of Mexico																	
Marco Island (Florida)									9	18	2	1			30	36.8	0.7*
Tampa (Florida)										3	18	3	1		25	38.1	0.7*x
St. Marks (Florida)										13	12	3			28	37.6	0.7xy
Gilchrist (Texas)								1	8	12	6				27	36.9	0.8y
Corpus Christi (Texas)									2	23	4				29	37.1	0.5
Brownsville (Texas)									4	15	9	1			29	37.2	0.7
colei-Yucatan																	
Progreso	1		13	22	2										38	30.6	0.7*
Rio Lagartos					9	14	10	2							35	33.1	0.9*x
Chiquila		1	16	16	7										40	30.7	0.8x
TOTAL	1	1	29	38	18	14	10	2							113	31.4	1.9

TABLE 5. Number of vertebrae in *Menidia* populations. An asterisk or an x, y or z next to consecutive populations indicates statistically significant ($p<0.01$) difference between mean values. Other such differences are indicated in the text.

Population	32	33	34	35	36	37	38	39	40	41	42	N	$\bar{X}$	s
beryllina-Atlantic (Florida)														
Jacksonville							1	8	9	12		30	40.1	0.9*
Deerfield						3	7	9	3			22	38.6	0.9*
Key Largo					2	16	13	2				33	37.5	0.7
peninsulae-Atlantic (Florida)														
Titusville							6	12	9	3		30	39.3	0.9
Sebastian Inlet							4	15	12	3	1	35	39.5	0.9
Fort Pierce							4	24	1	1		30	39.0	0.6*
conchorum-Florida Keys														
Long Key				1	4	8	16	1				30	37.4	0.9*
Grassy Key					2	15	7	1				25	37.3	0.7x
Big Pine Key			1	2	13	9	2					27	36.3	0.9x
Rockland Key					17	11	1					29	36.5	0.6
TOTAL			1	3	36	43	26	2				111	36.9	0.8
peninsulae-Gulf of Mexico														
Marco Island (Florida)							2	16	5	4		27	39.4	0.8
Tampa (Florida)							1	9	11	7	1	29	39.9	0.9*
St. Marks (Florida)									14	13	3	30	40.6	0.7*x
San Luis Pass (Texas)								13	13	3	1	30	39.2	0.8xy
Rockport (Texas)						1		3	18	8		30	40.1	0.8yz
Brownsville (Texas)							3	14	12	1		30	39.4	0.7z
beryllina-Gulf of Mexico														
Marco Island (Florida)						2	20	5	2			29	38.2	0.7*
Tampa (Florida)								13	12	1		26	39.5	0.6*
St. Marks (Florida)							5	9	15	1		30	39.4	0.8x
Gilchrist (Texas)						4	10	13	3			30	38.5	0.9x
Corpus Christi (Texas)						3	3	22	2			30	38.8	0.7
Brownsville (Texas)					1	4	9	12	3			29	38.4	1.0
colei-Yucatan														
Progreso	4	15	9	2								30	33.3	0.8*
Rio Lagartos			1	16	11		1					29	35.5	0.7*x
Chiquila	1	11	15	3								30	33.7	0.7x
TOTAL	5	26	25	21	11		1					89	34.1	1.4

INTRASPECIFIC VARIATION.—*Menidia beryllina*—Considerable inter-population variation exists with statistically different means between adjacent populations, i.e. Miami and Key Largo, and Key Largo and Marco Island, for anal fin rays; between Jacksonville and Deerfield, Miami and Key Largo, Key Largo and Marco Island, and Marco Island and Tampa for predorsal scale number; between Miami and Key Largo, Key Largo and Marco Island, and Marco Island and Tampa for lateral scale number; and between all adjacent Atlantic coast populations, and Key Largo and Marco Island, and Marco Island and Tampa for vertebral number. In general, there are sharp clinal patterns with decreasing counts southward on the Atlantic coast, but there is less marked variation in the Gulf of Mexico. There is not much similarity between Gulf of Mexico and Atlantic coast populations, and the southernmost population at Key Largo has markedly lower, statistically significant, counts for all traits.

Menidia peninsulae—Between population variation is less marked in this species than in *M. beryllina*. Atlantic coast populations are rather uniform for the traits studied. Statistically significant differences exist for all traits between eastern and western Gulf of Mexico populations, a fact also noted by Chernoff et al. (1981). Some differentiation between Gulf of Mexico and Atlantic populations is also indicated. North-south clinal patterns are not evident, in contrast to *M. beryllina*.

Menidia conchorum—Middle Florida Keys populations tend to have higher counts than lower Florida Keys populations. Some clinal gradation is evident, especially for lateral scale number. Middle and lower Florida Keys populations do differ at a significant level for predorsal scales and vertebral number. The data do not suggest, however, any more marked inter-population variation than occurs in *M. peninsulae*, and less than in *M. beryllina*.

Menidia colei—In all traits examined the Rio Lagartos population had markedly higher means than the Progreso and Chiquila populations. Based on these four traits alone, the Rio Lagartos population could certainly be recognized as specifically distinct from the other two. This is at odds with the electrophoretic data presented later in this paper, however, and no conclusion is drawn from the meristic data alone at this point. It should be emphasized that the meristic differences exhibited by the Rio Lagartos population (as compared to other *M. colei* populations) is no greater than that shown by the Key Largo population of *M. beryllina* (as compared to other *M. beryllina* populations).

The meristic variation exhibited by the above *Menidia* species is remarkable. It may reflect a considerable influence of environmental conditions on meristic traits during development, genetic drift or some especially strong local selection. Our data are in strong support of Chernoff et al.'s (1981) conclusion that *Menidia* are phenotypically plastic.

INTERSPECIFIC COMPARISIONS.—*Menidia beryllina* and *M. peninsulae*—Although a comparision of these species has been done by others (Johnson, 1975), we include brief observations which have a bearing on the relationship of *M. conchorum* to both species. Atlantic coast populations of *M. beryllina* and *M. peninsulae* taken as a whole have statistically different means for anal fin ray number, predorsal scale number and number of vertebrae. Key Largo populations of *M. beryllina* are more similar for anal fin rays and predorsal

scale number to *M. peninsulae* than to other *M. beryllina* populations. However, these Key Largo *M. beryllina* differ markedly from *M. peninsulae* in number of lateral scales and vertebrae. Gulf of Mexico populations of *M. beryllina* and *M. peninsulae* differ in number of predorsal and lateral scales, but meristic differences in general are not as great as between Atlantic coast populations of the two species.

Menidia beryllina and *M. conchorum*—Comparision of *M. beryllina* populations adjacent to *M. conchorum* involves comparision of Key Largo and Marco Island *M. beryllina* to Long Key *M. conchorum*. Key Largo *M. beryllina* differ significantly from Long Key populations in the number of anal fin rays and lateral scales, while Marco Island *M. beryllina* differ significantly from Long Key *M. conchorum* in all four traits presented here. For one trait, number of predorsal scales, Key Largo *M. beryllina* and Long Key *M. conchorum* are quite similar, but so is Ft. Pierce *M. peninsulae*. Of note is that *M. beryllina* from Key Largo, Ft. Pierce *M. peninsulae* and Long Key *M. conchorum* are all more similar to one another for the number of predorsal scales than middle Florida Keys *M. conchorum* are to lower Florida Keys *M. conchorum*. For number of vertebrae, Key Largo *M. beryllina* are also quite similar to *M. conchorum*, while *M. peninsulae* differs significantly from *M. conchorum* for this trait.

In summary, Key Largo *M. beryllina* are more similar in meristic traits to *M. conchorum* from Long Key than to *M. beryllina* from Marco Island, and middle Florida Keys *M. conchorum* are more similar to Key Largo *M. beryllina* than to lower Florida Keys *M. conchorum*. We feel that these counts are quite probably under environmental influence—different species (i.e. *M. beryllina* and *M. conchorum*) from the same or nearby localities are more similar than populations of the same species from different localities.

Menidia peninsulae and *M. conchorum*—The Fort Pierce (Atlantic coast) population of *M. peninsulae* is statistically different in the number of anal fin rays, lateral scales and vertebrae from Long Key *M. conchorum*. The same three traits distinguish Marco Island *M. peninsulae* from Long Key *M. conchorum*. The magnitude of these differences could be interpreted as that of species level differentiation, although clinal variation, with counts decreasing southward, is evident on the Florida Gulf coast. Electrophoretic data presented later, however, show no differences between *M. peninsulae* and *M. conchorum*.

Menidia colei and *M. conchorum, M. beryllina* and *M. peninsulae*—*Menidia colei* can be clearly distinguished from these three other species on the basis of all four traits presented. There is no basis, from meristic data, to conclude a closer relationship of *M. colei* to *M. conchorum* or to either *M. beryllina* or *M. peninsulae* populations from southern Texas.

In summary, meristic data clearly delineate *M. conchorum* from *M. colei* and to a lesser degree from *M. beryllina* and *M. peninsulae*. *Menidia conchorum* is as different from *M. peninsulae* in meristic traits as it is from southernmost *M. beryllina* populations. In fact, middle Florida Keys *M. conchorum* are more similar overall to Key Largo *M. beryllina* then to either *M. peninsulae* or lower Florida Keys *M. conchorum*, indicating an environmental influence on meristics. This statement ignores, however, the north-south clinal trends in *M. conchorum* and *M. peninsulae* and the allopatry of *M. conchorum* and *M. beryllina*.

The only decision relative to *M. conchorum* that can be made with these

TABLE 6. Electromorph frequencies in *Menida* (Population symbols: co=*M. colei*, cm=*M. conchorum*, p=*M. peninsulae*, b=*M. beryllina*, m=*M. menidia*).

		co	1cm	2cm	3cm	4cm	5cm	6p	7p	8p	9p	10p	11p	12p
Gpi-A	*a*				0.03			0.12	0.03		0.12			
	b	0.04		0.70	0.10	0.70	0.05	0.65	0.17	0.17	0.58	0.23	0.07	0.15
	c	0.96	0.55	0.20	0.80	0.27	0.90	0.20	0.50	0.53	0.25	0.50	0.50	0.77
	d		0.45	0.10	0.07	0.03	0.05	0.03	0.30	0.30	0.05	0.23	0.38	0.08
	e											0.04	0.05	
Gpi-B	*a*											0.03	0.03	
	b					0.08					0.05	0.03	0.03	0.05
	c	1.0	0.80	1.0	1.0	0.84	0.68	1.0	1.0	1.0	0.95	0.94	0.94	0.95
	d		0.20			0.08	0.32							
AK	*a*													
	b	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Est-3	*a*													
	b	1.0	0.13		0.15	0.15	0.13				0.05	0.05		
	c		0.87	1.0	0.85	0.80	0.63	1.0	1.0	1.0	0.75	0.95	1.0	1.0
	d					0.05	0.24				0.20			
	e													
Gp-1	*a*	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	b													
Gp-2	*a*		1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	
	b	1.0												1.0
Gp-3	*a*													
	b	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
M-Icdh-A	*a*		1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	b	1.0												
S-Icdh-A	*a*													
	b		1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	c	1.0												
Pgm-B	*a*													
	b													
	c													
	d			0.05		0.20						0.10		
	e				0.03				0.10		0.03		0.03	
	f	0.98	1.0	0.93	0.97	0.70	1.0	1.0	0.85	1.0	0.97	0.85	0.97	0.05
	g	0.02		0.02		0.10			0.05			0.05		0.95

meristic data is that *M. conchorum* is a distinct allopatric species, a decision that is at odds with the electrophoretic data that follow. The overall high level of intraspecific variation with *Menidia* meristic data renders this conclusion suspect, in our opinion, and must be tempered by analysis of the electrophoretic data.

Electrophoretic Variation.—Of the 27 loci coding for proteins surveyed in this study, 5 (Gp-4, Adh, GA-3-pdh, Sod and Ldh-C) were fixed for the same electromorph in all samples. For an additional four loci (Ldh-A,B, S-Mdh-A and Pgdh-A) the same electromorph was found in at least 98% frequency in all samples; these four loci are also con-

TABLE 6. (Continued)

13p	14b	15b	16b	17b	18b	19b	20b	21b	m
		0.25	0.52	0.03		0.02			
0.17	0.05	0.03		0.93	0.58	0.42	0.15		0.15
0.63	0.48	0.48	0.48	0.04	0.40	0.50	0.80	1.0	0.05
0.20	0.45	0.24			0.02	0.06	0.05		0.75
	0.02								0.05
	0.03								0.93
0.05	0.20						0.03		0.07
0.93	0.77	0.90	0.98	0.95	1.0	1.0	0.97	1.0	
0.02		0.10	0.02	0.05					
	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
1.0									
	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	
1.0									
									1.0
1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	
									1.0
1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
									1.0
1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	
1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
									1.0
1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	
									0.5
									0.5
	0.05				0.20				
	0.95	1.0	1.0	1.0	0.80	1.0	0.90	1.0	
							0.10		
1.0	0.05								

sidered monomorphic. Electromorph frequency variation was observed for the remaining 18 loci studied. In six of the polymorphic loci (G-3-pdh-B, S-Mdh-B, Pgm-A, Xdh-A,B and GA-3-pdh-C) there was only slight electrophoretically detectable variation. The common shared electromorph frequency varied from fixation to 63%. These above loci are not presented in tabular form. For two loci (Gldh and Est-1) no single electromorph was the most common in all samples. The number of observed electromorphs per locus varied from four (Gldh) to six (Est-1). Unique, rare and semi-rare, frequencies less than 25%, electromorphs were found only in populations of *M. beryllina*. Although populations of *M. conchorum* were variable for Gldh, they

possessed no electromorphs that were not also found in either *M. peninsulae* or *M. beryllina*. Data for these loci are also not presented in tabular form.

Electromorph frequencies for Gpi-A,B demonstrated marked perturbations among samples. A rare electromorph (*a*) for Gpi-B was found at a nearly fixed difference level in *M. menidia* (93%). *Menidia conchorum* and *M. peninsulae* were similar for Gpi-A,B. (Table 6).

Alternative species specific electromorphs were found for Ak, Gp-1,2,3, M-Icdh-A, S-Icdh-A, Pgm-B and Est-3 (Table 6). *Menidia beryllina* was completely differentiated from all other samples by electromorphs for Est-3 and from all except *M. menidia* by Ak. In addition, Pgm-B affords a nearly fixed difference from *M. peninsulae* (and *M. conchorum*). As noted by Johnson (1975), Texas populations of *M. peninsulae* share the otherwise species specific Gp-2 (*b*) electromorph found in *M. beryllina*. Although the above three (or four including Gp-2) loci clearly differentiate *M. beryllina* and *M. peninsulae*, no species specific electromorphs were found to differentiate *M. peninsulae* and *M. conchorum*. There is no evidence from the genetic data to suggest *M. conchorum* hybridizes with *M. beryllina;* no heterozygotes were observed for Ak, Gp-2 or Est-3. No evidence was found to suggest that *M. conchorum* and *M. peninsulae* were differentiated to the degree that hybridization could be detected by electrophoretic analysis.

Menidia menidia is completely differentiated by Est-3, Gp-1,3, S-Icdh-A and Pgm-B from other *Menidia*. *Menidia colei* is differentiated from all other populations by M-Icdh-A, S-Icdh-A and shows marked frequency differences from other *Menidia* species at Est-3. Three populations of *M. colei* were analyzed and showed virtually no interpopulation variation (D=0.008). In summary, *M. conchorum* differs from *M. beryllina* and *M. colei* at four loci, and from *M. menidia* at eight. However, *M. conchorum* and *M. peninsulae* do not have any fixed differences and show no indication of major gene frequency differences.

Because closely related species that have begun to diverge may be differentiated by only subtle differences in gene frequencies (Ayala et al., 1974; Avise, 1974; Mayr, 1963), genetic distance estimates, D, were calculated from the electromorph frequency data. Values for pairwise comparisions within and between species are reported in Table 7. Interspecific values ranged from 0.027 (*M. conchorum* vs. *M. peninsulae*) to a maximum of 0.394 (*M. colei* vs. *M. menidia*). The genetic distance of *M. colei* to *M. peninsulae*, *M. conchorum*, and *M. beryllina* was 0.177, 0.205, and 0.241, respectively. *Menidia colei* is not clearly more closely related to one than the other, and certainly there is no evidence from biochemical data that *M. colei* and *M. conchorum* are especially closely related and should be separated into another genus.

TABLE 7. Mean genetic distance within and between 5 species of *Menidia*.

	colei	*conchorum*	*beryllina*	*peninsulae*	*menidia*
colei	0.005±0.004	0.205±0.007	0.241±0.031	0.177±0.005	0.394±0.013
conchorum		0.024±0.011	0.195±0.024	0.027±0.022	0.383±0.02
beryllina			0.028±0.013	0.200±0.102	0.285±0.04
peninsulae				0.027±0.021	0.373±0.05
menidia					—

The average standard genetic distances ($\bar{D}$) within taxa were small and consistent: $\bar{D}$=0.024± 0.011 for *M. conchorum;* 0.027± 0.021 for *M. peninsulae;* 0.028± 0.013 for *M. beryllina,* and 0.005± 0.004 for *M. colei.* The $\bar{D}$ values between either *M. conchorum* or *M. peninsulae* and *M. beryllina* ($\bar{D}$=0.195± 0.024 and 0.200± 0.013 for *M. conchorum* and *M. peninsulae* vs. *M. beryllina,* respectively), were similar and an order of magnitude greater than within taxa values. However, $\bar{D}$ values between *M. conchorum* and *M. peninsulae* ($\bar{D}$=0.027± 0.022) were an order of magnitude smaller than the values observed between other taxa. This smaller value is on the order of values observed between conspecific fish populations (Avise, 1974).

We interpret these results to corroborate the initial genetic result, that of no genetic differentiation between *M. conchorum* and *M. peninsulae.* We and others (Johnson, 1975) have demonstrated that *M. peninsulae* and *M. beryllina* are readily distinguishable species based on biochemical characters and we observe large average genetic distances between them (D=0.200). On the other hand, no species specific electromorphs were found to differentiate *M. conchorum* from *M. peninsulae,* and both of these forms are differentiated from *M. beryllina* by the same set of traits. The smallest genetic distance values were observed between *M. conchorum* and *M. peninsulae.* Furthermore, the observed genetic distance values between these nominal species were on the order expected and observed between conspecific populations.

Systematic Conclusions

Johnson (1975) studied morphological and electrophoretic characters in five species of *Menidia.* He concluded that *M. peninsulae* and *M. beryllina* were sibling species, but he did not consider the systematic position of *M. conchorum.* He followed Miller (1976) and accepted the view that Key Silversides were rare and restricted to the lower Florida Keys. As noted earlier, our field collections revealed populations of *M. conchorum* in the middle Florida Keys (Long and Grassy Keys), thus suggesting a more wide-spread and northerly distribution than previously recognized.

The possibility that the populations of *M. conchorum* we found in the middle Florida Keys represent recently founded or introduced populations should be considered. However, we know of no basis for such an assumption. In such cases of founder populations, a genetic "bottleneck" may be created and heterozygosity is depressed as compared to long established populations (Soule, 1976). We calculated average individual heterozygosity H (Soule and Yang, 1973) for *M. conchorum* and the populations of the other species of *Menidia* examined in this paper. Average heterozygosities (Table 8) in all species populations ranged from 1.13% (Brownsville, Texas population of *M. beryllina*) to 10.20% (Tampa, Florida population of *M. peninsulae*); the heterozygosities for Grassy Key (2.88%) and Long Key (4.11%) were not depressed. Based on the robustness of the middle Florida Keys populations as observed in the field and the lack of depressed heterozygosities, we conclude that there is no evidence that middle Florida Keys populations of *M. conchorum* represent newly founded populations. We suggest collecting efforts in the past were inadequate, and that other, as yet undiscovered northern populations and populations on outlying Florida Keys, exist.

TABLE 8. Heterozygosity values for populations of four species of *Menidia*.

Locality	Population No.	H
colei		
Progreso	A	1.88
Rio Lagartos	B	1.20
Chiquila	C	3.60
peninsulae (formerly *conchorum*)		
Long Key	1	4.11
Grassy Key	2	2.88
Big Pine Key	3	4.62
Cudjoe Key	4	5.40
Rockland Key	5	5.74
peninsulae		
Titusville	6	3.70
Sebastian Inlet	7	6.35
Ft. Pierce	8	3.33
Marco Island	9	6.32
Tampa	10	10.20
St. Marks	11	4.04
San Luis Pass	12	5.00
Brownsville	13	5.28
beryllina		
Jacksonville	14	7.58
Deerfield	15	7.22
Key Largo	16	5.56
Marco Island	17	4.60
Tampa	18	8.46
St. Marks	19	4.44
Gilchrist	20	4.11
Brownsville	21	1.13
menidia		
Jacksonville	22	6.01

We reach the following conclusions:

1. *Menidia conchorum* and *M. peninsulae* differ on the basis of meristic features to a level that could by traditional taxonomic analysis be considered distinct species. However, these nominal species show no differences in any of 27 electrophoretic traits examined, suggesting that the observed meristic variation in both *M. peninsulae* and the nominal *M. conchorum* could be due to environmental effects on the phenotype. Of note is the considerable meristic variation throughout *Menidia* that is evident in Tables 2-5 (and see Chernoff et al., 1981). In fact, based on the four meristic characters presented here, there is nearly as much justification to recognize the Rio Lagartos population of *M. colei* and the Key Largo population of *M. beryllina* as distinct species as there is to consider *M. conchorum* distinct. We believe, as did Chernoff et al. (1981) that much of the meristic variation in *Menidia* is due to environmental influences, as evidenced by north-south clinal variation and similar meristic counts in different species from the same or nearby localities. Such variation is not evident for the electrophoretic traits. This wide meristic variation, we believe, has masked the genetic similarity of *M. conchorum* and *M. peninsulae* in previous studies. In this case, the electrophoretic data are, in our opinion, more reliable and strongly suggest that *M. conchorum* is conspecific with *M. peninsulae*. We temper our conclusion, however, because we recognize that although two forms can be proven different, it is impossible to prove that they are the same, because one can never examine all possible characters. Nevertheless, we feel that *M. peninsulae* and *M. conchorum* are conspecific. The name *M. peninsulae* has nomenclatural priority.

2. *Menidia beryllina* and *Menidia peninsulae* are distinct species, as demonstrated earlier by Johnson (1975). *Menidia conchorum* differs electrophoretically from *M. beryllina* in the same ways that *M. peninsulae* does.

3. *Menidia colei* is not more closely related to *M. conchorum* than it is to other *Menidia* species, thus invalidating Schultz's (1948) suggestion that they should be grouped together in the genus *Menidiella*.

4. *Menidia conchorum* is more widespread than previously thought; the newly discovered populations do not appear to be recently founded.

ACKNOWLEDGEMENTS

We thank Dr. Robert R. Miller for valuable suggestions and assistance in

obtaining permits to collect fishes in Mexico, and Drs. J. C. Avise, D. G. Buth, C. R. Gilbert, C. R. Robins, and L. Rivas for their assistance. Special appreciation is due C. Teaf for many hours of field assistance. In addition, we are grateful to the following persons for field assistance: R. Cowdery, W. Giesy, S. Harding, D. and E. Leslie, C. Mesing and G. Relyea. We thank the Fish and Wildlife Commissions of Texas and Mexico for their cooperation in providing collecting permits. This study was supported in part by a Grant-in- aid of Research from Sigma Xi, and a grant from the Smithsonian Institution L. P. Schultz fund.

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Geographic Variation in Gulf Slope Populations of the Bluntnose Darter, *Etheostoma chlorosomum* (Hay)

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Abstract

A total of 452 specimens of the bluntnose darter, *Etheostoma chlorosomum* from throughout the Gulf Slope portion of its range was examined for geographic variation in several morphological characters. Significant variation occurred in scale counts, the lateralis system, fin and branchiostegal rays, and body squamation, with the latter exhibiting the strongest patterns of geographic variation. Western populations (Colorado River, Texas) showed a consistent divergence with significantly higher means for otherwise conservative characters. However, there was little evidence to support the taxonomic recognition of any group of Gulf Slope populations of *E. chlorosomum*. Variation in *E. davisoni* is included for comparison. Relationships within *Vaillantia* and evolution of the group are discussed.

Introduction

The bluntnose darter, *Etheostoma chlorosomum*, is a widely distributed species found throughout much of the Mississippi River Valley and along the Gulf Coast (Gilbert, 1980). Despite its wide occurrence and relatively long history in the taxonomic literature, the bluntnose darter remains poorly known in many parts of its range. This study was undertaken to characterize the variation of the species over the southern part of its range (along the Gulf Slope), to compare morphological features for populations in the coastal drainages, and to classify relationships between *E. chlorosomum* and its reported closest relative, *E. davisoni*, the Choctawhatchee darter.

Nomenclatoral History and Relationships

The species was originally described as *Boleosoma camurum* by Forbes in 1878 from specimens collected in the Illinois River drainage, Illinois (Collette and Knapp, 1967). In 1881, Hay described *Vaillantia chlorosoma* from a tributary to the Tuscumbia River in Mississippi. Jordan and Gilbert (1883) recognized the similarity between *B. camurum* and *V. chlorosoma* and assigned *B. camurum* to *Vaillantia*. Bailey and Gosline (1955) recognized just one valid species, *Etheostoma chlorosomum* (the earlier name *camurum* was preoccupied in *Poecilichthyes*), which they assigned to the subgenus *Boleosoma*. Cole (1967) reallocated *E. chlorosomum* to the subgenus *Vaillantia* because the species exhibited character states that were inconsistent with other members of *Boleosoma*.

In addition to the bluntnose darter, the subgenus *Vaillantia* presently includes *E. davisoni*, which was resurrected from the synonomy of *E. stigmaeum* by Howell (1968). Although *E.*

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chlorosomum has been considered in a number of taxonomic revisions, this study represents the first in depth treatment of variation and relationships for the species.

Page (1981) grouped *Vaillantia* with five other subgenera, including *Etheostoma, Nanostoma, Doration, Boleosoma,* and *Ioa.* Members share a tendency toward reduction of characters. Although *E. chlorosomum* and *E. davisoni* failed to cluster in phenograms, Page (1981) argued that *Vaillantia* should be retained due to important synapomorphies.

Distribution

The bluntnose darter is distributed in the Mississippi River basin from Minnesota southward to Louisiana, occurring in the lowlands and plains as far west as Oklahoma and to Indiana in the east (Gilbert, 1980). The species is also widely distributed across Gulf Coastal drainages east and west of the Mississippi River, where it is primarily restricted to low-gradient, Coastal Plain situations (i.e., below the Fall Line, Fig. 1). West of the Mississippi River *E. chlorosomum* occurs across coastal streams to the Colorado River drainage in Texas. Eastward the species occurs in major coastal streams from Louisiana to the Mobile Bay basin in Alabama. East of Mobile Bay, the the bluntnose darter is replaced by the Choctawhatchee darter, *E. davisoni,* which is confined to drainages of Pensacola and Choctawhatchee bays. Throughout its range, the bluntnose darter inhabits sluggish, low gradient streams, lower channels of large rivers, sloughs, backwaters and small lakes. The species prefers sandy to muddy bottomed streams with slight flow.

Pflieger (1971) classified *E. chlorosomum* as a lowland species, autochthonous to the central Mississippi Valley. This region is the apparent center of distribution and perhaps the center of origin as well. The bluntnose darter has undoubted followed the Mississippi Valley in its dispersal, except for its invasion of Gulf Slope drainages. There it likely crossed several southward flowing streams as it spread east and west. Populations of *E. chlorosomum* occurring in these streams are presently isolated from the more continuously distributed populations in the Mississippi River basin. In the case of *E. davisoni,* isolation in coastal streams was sufficiently long for speciation to occur. Thus, we expected variation to be most pronounced among Gulf Slope populations of the bluntnose darter, and therefore concentrated on this portion of its range. Data on variation of *E. davisoni* (included for comparison) was kindly provided by W. M. Howell (based on Howell, 1968).

Material Examined

Numbers in parentheses following major drainages are the total number of specimens examined and are applicable to the drainages listed in figures 3-9. Numbers in parentheses following museum numbers indicate specimens examined from that collection. Museum acronyms are identified in the acknowledgments.

Colorado River Drainage (6): Texas, Colorado Co., TU 73402 (5) Cummings Creek 0.5 mi above confluence with Colorado River; Travis Co., TNHC 1068 (1) Colorado River at Austin. Brazos River Drainage (12): Texas, Grimes Co., TNHC 8544 (8) Sulfur Creek 2.5 mi SW Singleton; TNHC 8511 (4) Gibbons Creek 2 mi NW Carlos. San Jacinto River Drainage (30): Texas, Harris Co., TU 66493 (20) Willow Creek at rear North Hampton subdivision; Montgomery Co., TU 61898 (10) San Jacinto River at FM 2854, 3 mi W Conroe. Trinity River Drainage (8): Texas, Liberty Co., TU 70123 (1) Trinity River at FM 1620, 5.3 mi W Moss; San Jacinto Co., TU 66447 (7) Big Creek at Texas Hwy 150, 2.3 mi N Shepard. Neches

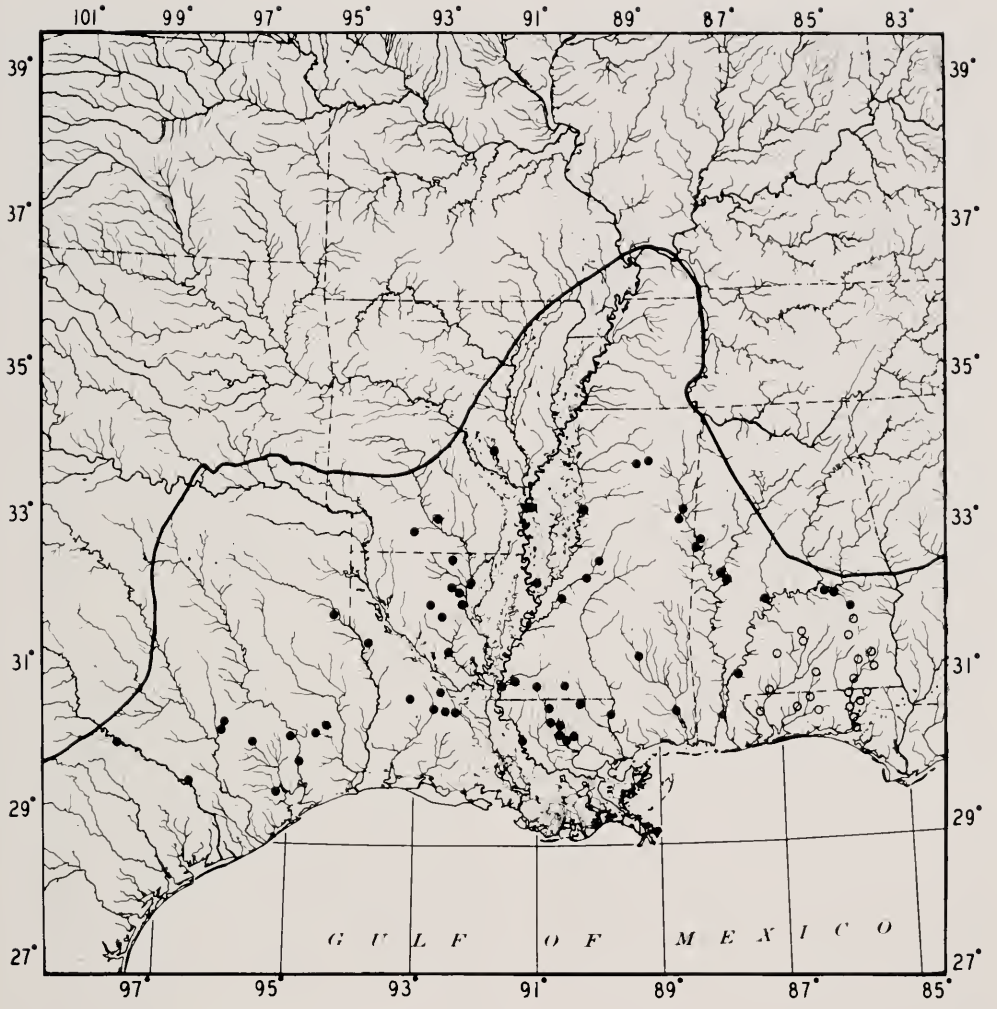

Fig. 1. Gulf Slope Region and its northern boundary, represented by the geographic Fall Line (heavy line), sample sites for *Etheostoma chlorosomum* populations (solid circles), and the distribution of *E. davisoni* (open circles).

River Drainage (31): Texas, Polk Co., TU 106050 (9) Big Sandy Creek, 3.5 km SE Camp Ruby, FM 1276; Tyler Co., TU 21457 (22) Little Cypress Creek at Rte 287, 6 mi N Woodville. Sabine River Drainage (25): Texas, Panola Co., CU 34924 (2) trib 2.8 mi NE Carthage, Rte 79; Louisiana, Sabine Par., TU 4566 (23) trib to Bayou San Patricia 4.4 mi NW Noble Hwy 171. Calcasieu River Drainage (36): Louisiana, Allen Par., TU 43299 (30) Calcasieu River at Hwy 10, 2 mi W Oakdale; Vernon Par., NLU 4437 (6) Calcasieu River at Hwy 339, sec 9, T1S, R7W. Mermentau River Drainage (5): Louisiana, Evangeline Par., TU 41473 (4); TU 44568 (1) Boggy Bayou at Hwy 106, 3 mi W Hwy 13. Vermilion-Teche River Drainage (23): Louisiana, Evangeline Par., TU 87389 (2) Lake Chicot at Chicot Park, sec 21, R2E, T3S; Rapides Par., TU 40013 (15); TU 50150 (6) trib to Bayou Cocodrie at Hwy 12, 1 mi E Melder. Little River Drainage (5): Louisiana, Grant Par., NLU 3273 (5) Fish Creek at Rte 123, sec 27, T8N, R1W; Jackson Par., TU 55132 (2) Dugdemona River 0.3 mi S Quitman; NLU 3708 (8) Flat Creek sec 30, T16N, R1W. Ouachita River Drainage (26): Louisiana, Ouachita Par., NLU 1439 (2) Edgewater Dam-Bayou at Desaird, sec 40, T1N, R4E; NLU 2827 (4) Cypress Creek, sec 5, T15N, R2E; NLU 3552 (5) Choudrant Bayou, sec 16, T18N, R1E; NLU 3553 (4) South Chenniere, sec 4, T16N, R1E; Union Par., NLU 2967 (4) Meridian Creek, sec 33, T23N, R1E; Arkansas, Cal-

houn Co., TU 97748 (3) Focus Creek at Hwy 4, 1 mi NW Focus Bayou; Columbia Co., TU 84264 (2) trib to Smackover Creek at Hwy 98, sec 2, T16S, R20W; TU 84254 (2) Sloan Creek, 8 mi NE Magnolia. MISSISSIPPI RIVER BASIN (11): Louisiana, West Baton Rouge Par., TU 112533 (7) Mississippi River at river mi 252; Mississippi, Issaquena Co., TU 48286 (1) Steele Bayou at Hwy 1, 4.6 mi W Onward; Bolivar Co., TU 86036 (1) Lake Whittington 2 mi W Benoit; Wilkinson Co., TU 71178 (1) Piney Creek at Hwy 563, 4.2 mi E Wilkinson; TU 86254 (1) Lake Mary 14.7 air mi NW Woodville. ARKANSAS RIVER DRAINAGE (30): Arkansas, Arkansas Co., TU 97370 (20) Crooked Creek at Hwy 79, 10 mi SW Stuttgart; TU 2219 (10) trib to Bayou Meto 2 mi N Humphrey. BIG BLACK RIVER DRAINAGE (30): Mississippi, Holmes-Attala Co., TU 88220 (11) Big Black River at Pickens, Hwy 17; Hinds Co., TU 75443 (9) Porter Creek 9.5 mi. NE Edwards; Madison-Yazoo Co., TU 73064 (10) Big Black River at Hwy 16, 4 mi WNW I-55. YAZOO RIVER DRAINAGE (6): Mississippi, Lafayette Co., TU 87649 (3) Little Kettle Creek at Hwy 334, 7.3 ml W Toccopoda; Pontotoc Co., TU 87623 (2) Mud Creek at Hwy 334 1.1 mi W of Springville; Mississippi, Tallahatchie Co., TU 86102 (1) Slough of Tallahatchie at Hwy 8, River E of Phillip. AMITE RIVER DRAINAGE (21): Louisiana, Livingston Par., UNO 2525 (10, 40-45) Colyell Creek at Hwy 1024, 3 mi S I-12; St Helena Par., NLU 1118 (2); NLU 1119 (5) Birch Creek at Rte 448, sec 82, T2S, R4E; Mississippi, Amite Co., UAIC 1576 (2) Little Beaver Creek at Hwy 23, 4 mi E Centreville, sec 26, T1N, R2E; Lincoln Co., TU 76079 (2) East Branch of East Fork Amite River 2.6 mi W Arlington. TICKFAW RIVER DRAINAGE (30); Louisiana, Livingston Par., NLU 4120 (23) Blood River, sec 24, T5S, R5E; TU 3807 (1) Big Branch of Hog Branch 0.8 mi W Holden at Rte 190; TU 83128 (2) West Hog Branch at Hwy 442, 13.2 mi W Tickfaw; St Helena Par., NLU 3732 (4) West Hog Branch sec 70, T4S, R4E. NATALBANY RIVER DRAIANGE (7): Louisiana, Tangipahoa Par., NLU 1002 (4) Pontchatoula Creek at Rte 190, E Hammond sec 19, T6S, R8E; TU 86459 (2) Natalbany River 4.2 mi W Hammond, at I-12; TU 4440 (1) trib to Natalhany River 3.1 mi W Hammond at Rte 51. TANGIPAHOA RIVER DRAINAGE (8): Louisiana, Tangipahoa Par., CU 13948 (4) trib to Selser Creek 3.3 mi E Hammond al Rte 190; Mississippi, Pike Co., UNO 521 (1) Tangipahoa River 2.1 mi W Magnolia; TU 67116 (3) Tangipahoa River 0.7 mi S Magnolia. PEARL RIVER DRAINAGE (31): Louisiana, Tangipahoa Par., NLU 1009 (1) Wilson's Branch at Hwy 38, 12 mi E Kentwood sec 39, T1S, R8E; Washington Par., TU 39678 (30) Pearl River at Pools Bluff, 4 mi S Bogalousa. PASCAGOULA RIVER DRAINAGE (11): Mississippi, George Co., TU 100183 (10) Pascagoula River at Hwy 26; Jones Co., TU 84718 (1) Leaf River below Rte 84. TOMBIGBEE RIVER DRAINAGE (41): Mississippi, Lowndes Co., UAIC 1786 (6) trib to Catalpa Creek, sec 33, T19N, R16E; TU 54805 (3) Tombigbee River at Hwy 50, 9 mi NW Columbus; Alabama, Greene Co., UAIC 1898 (4) Taylor Creek 2.1 mi W Rte 43; TU 76896 (12) Taylor Creek 4.7 mi S Boligee; UAIC 696 (1) Needham Creek, sec 5, T20N, R2E; TU 76976 (3) Needham Creek 4.4 mi N Demopolis; TU 76856 (3) trib to Tombigbee River., 2.5 mi SW Forkland; CU 21899 (1) trib 11 mi N of Black Warrior at Hwy 40; Pickens Co., UAIC 1892 (1) Beaver Creek at Hwy 14, 4.4 mi NW Aliceville; TU 76997 (1) Beaver at Hwy 14 Creek 5.2 mi SE of Pickensville; Sumpter Co., TU 48920 (2) Noxubee Creek at Hwy 17 4.4 mi N Gieger; TU 85729 (4) Tombigbee River 3 mi N Gainsville. ALABAMA RIVER DRAINAGE (10): Alabama, Dallas Co., UAIC 2394 (3) Tatum Creek 2.5 mi N Orville; Monroe Co., TU 114915 (1) Alabama River along right bank at river mi 102; TU 44426 (2) Little River 13.1 mi W Uriah, at Hwy 59; Montgomery Co., UAIC 1510 (1) Johnson's Creek W Montgomery sec 18, T15N, R21E; UAIC 1238 (1) Miller Cr. at I-85, 2 mi E Mt Meigs; Bullock Co., UAIC 1483 (2) trib to Slaughter Creek 0.5 mi N Thompson sec 23, T14N, R22E.

METHODS

In order to reduce sample bias, drainages were represented by as many localities as the material allowed, rather than large series from a single locality. An effort was made to obtain at least 30 specimens per drainage but due to the limited amount of material available, this was not always possible. To lessen the effects of developmental variation, counts were limited to specimens above 30 mm in standard length (Collette 1962).

Counts were made following the methods of Hubbs and Lagler (1958), except as noted below. Scale rows in transverse series were counted according to Howell (1968). The cephalic canals of the lateralis system were examined following Hubbs and Cannon (1935), with special reference to cephalic canal patterns discussed by other authors (Cole, 1967; Page, 1977; Burr, 1978). Squamation of the nape, breast, anterior belly, head and prepectoral regions was scored according to the methods of Cole (1957, 1967) and Howell (1968).

Sex was determined primarily by examination of the genital papillae. Specimens were also examined for breeding tubercles and other sexually dimorphic characteristics. Intrapopulational variation in morphological characters was analyzed to determine if significant differences existed between sexes. The t test was used to determine significance.

Statistical Techniques

All statistical computations were performed on the University of New Orleans Computer System using the DEC system 10/20 version of the SPSS batch system. The SPSS subprograms used were CONDESCRIPTIVE (a package of descriptive statistics) and ONEWAY (oneway analysis of variance). A multiple range test using the Student Newman Keuls (SNK) procedure was conducted to assign statistical significance to group separations. SNK produced a series of homogeneous subsets of groups whose highest and lowest means did not differ by more than the shortest significant range for a subset of that size (Nie et al., 1975). In the graphs (Figs. 10 & 11) the means were arranged from highest to lowest value on the lower axis. Above each subset means were arranged in geographic sequence from east to west.

Graphical analyses of morphological characters follow Hubbs and Hubbs (1953). The analyses were performed with ranges, means, standard deviations, and standard errors from frequency distributions.

Character Selection

Originally, Gulf Slope populations of the bluntnose darter were scored for approximately 30 morphological characters. The character set was later reduced by eliminating invariant or redundant characters. This report is based on variation in 13 characters, including those used to delimit taxa in previous studies of percid systematics. However, it was not clear from these studies which characters would be most important for separating groups.

Collette (1962) stated that the number of pored lateral line scales was valuable in distinguishing subspecies of the swamp darter, *Etheostoma fusiforme*, while total lateral line scales was valuable in distinguishing some species of the subgenus *Hololepis*. Burr (1978) found that species in the subgenus *Microperca* could be separated based on pored lateral line scales. Cole (1967) based separation of subspecies of the tesselated darter, *E. olmstedi*, on total lateral line scales and percent squamation. Tsai and Raney (1974) used only total lateral line scales to separate the banded darter, *E. zonale*, into subspecies, stating that separation based on percent squamation was meaningless.

It was evident very early in our study that squamation of the breast and anterior belly showed considerable geographic variation among Gulf Slope populations of *E. chlorosomum* (Fig. 8). Other characters, including total lateral line scales, pored lateral line scales, caudal peduncle scale rows, nape squamation, and branchiostegal rays, showed either continuous variation from one population to the next, or varied abruptly after appearing nonvariable. Finally, characters such as anal rays, dorsal rays, and branched caudal rays showed little variation across the Gulf Slope range of the species.

Results

Etheostoma chlorosomum is a species of the subgenus *Vaillantia*, distinguished from the only other member, *E. davi-*

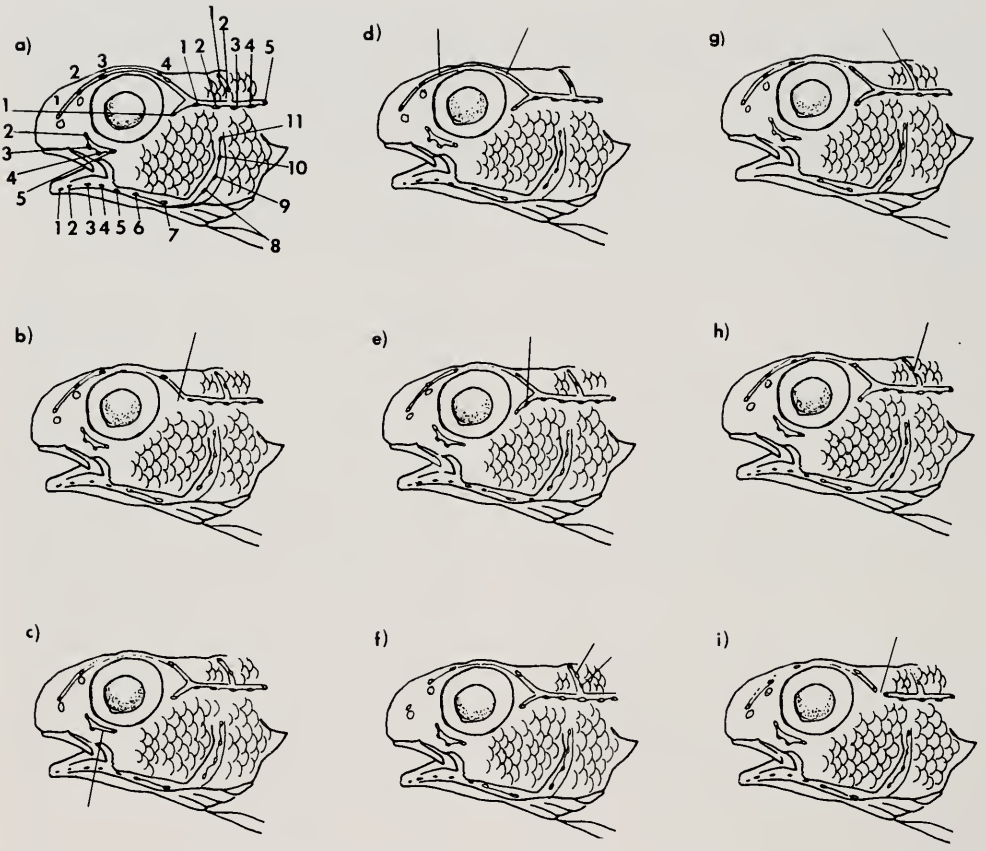

Fig. 2. Variation in development of the cephalic lateralis system in Gulf Slope populations of *Etheostoma chlorosomum*. a) Typical condition with numbers of pores and breaks in canals indicated. b,h & i) Deletions of portions of canals. c & d) Deletions of pores. e & f) Additions of pores. g) supratemporal canal complete across nape.

soni, by the morphology of the genital papillae of breeding females, the presence of breeding tubercles and having only one anal spine (Howell, 1968). It differs from all members of the subgenera *Boleosoma* and *Doration* in the morphology of the female genital papillae (Cole, 1967). The following results are based on an examination of 452 specimens from the Gulf Slope range of *E. chlorosomum*.

Along the Gulf Coast, *E. chlorosomum* is characterized by an incomplete lateral line, not arched upward anteriorly; 47-64 scales in lateral series of which 1-41 are pored; 10-17 scales in transverse series; 15-23 caudal peduncle scale rows. Fin rays: dorsal VII to XII (usually VIII to X), 8 to 13; anal I (rarely II), 6 to 11 (usually 8 or 9); branched caudal 11 to 15 (usually 13); total pectoral 24 to 30 (usually 26); pelvic I, 5 (always). Branchiostegal rays total 9 to 12 (usually 10), membrane slightly connected across isthmus.

The cephalic lateralis system displays random and developmental variation in number of pores and completeness of canals (Fig. 2). Infraorbital canal usually interrupted (Page, 1977), with 4 pores above the angle of the jaw and one behind the eye near the branch of

the lateral canal; lateral canal usually complete with 5 pores (incomplete in only one case); supratemporal canal complete across the head (2 pores) or interrupted laterally (3 pores); supraorbital canal always complete with 4 pores or with the number of pores reduced to 2 or 3; coronal pore present or absent; preoperculomandibular canal complete (9 pores) or interrupted (10 to 12 pores).

Squamation of the body shows considerable geographic variation. Nape in western populations between 0-100% scaled (means from 0-40%); lower Mississippi River populations east through Lake Pontchartrain drainages with between 0-100% scaled nape (means 30-70%); Pearl and Pascagoula populations have less than 5% scaled nape; easternmost populations 20-50%. Breast squamation higher (70%) in extreme west; lower in Brazos population (20%) and increasing clinally to 100% in the lower Mississippi and Pontchartrain populations; less than 10% in the Pearl and Pascagoula; and between 70-100% in eastern most populations. Anterior belly scaled 50% in western most population; lower in Brazos; increasing clinally to 100% in central Gulf Slope populations; virtually scaleless in Pearl and Pascagoula; and between 70-100% scaled in extreme eastern populations. Cheek and opercle always fully scaled.

There is little variation in coloration and pigmentation along the Gulf Slope. Juveniles and nonbreeding adults are pale yellow to straw colored dorsally and somewhat lighter ventrally. In life the body is greenish-yellow and transparent with olive-brown markings. The opercle and cheek has an iridescent blue-green hue. The body of preserved specimens is marked with zig-zagging brown blotches which irregularly form X's or M's on the sides, giving the appearance of a broken lateral stripe. The dorsum is crossed by six brown saddles separated by wider unpigmented interspaces. On the head, a faint suborbital bar extends from the orbit to the edge of the preoperculum. A postorbital blotch is usually visible near the posterior margin of the orbit on level with the pupil. A brown preorbital bar originates at the anterior edge of the orbit and continues around the snout, narrowing and being reflected ventrally onto the premaxilla. This feature is important in the diagnosis of *Vaillantia*. A frenum is usually absent, however, in some western populations there is a slight degree of connection between the tip of the snout and the premaxilla.

Geographic Variation

Populations of *E. chlorosomum* from more northern drainages of the Mississippi River were little different from those in lower Mississippi River drainages. All of these populations were characterized by high squamation, and they displayed similar variation in other characteristics. While the survey of northern populations was not exhaustive, it suggested little divergence within the Mississippi River Basin. Divergence was observed in populations from Gulf Slope drainages east and west of the Mississippi River. The patterns of geographic variation discussed below are based on comparisons of divergent Gulf Slope populations with populations from the lower Mississippi River basin.

Distinct patterns of variation were noted for four suites of characters: lateralis system (cephalic and lateral line), scale counts (lateral line and circumferential series), squamation, and ray counts (fin rays and branchiostegals). Fin ray characters were the most conservative. With the exception of the

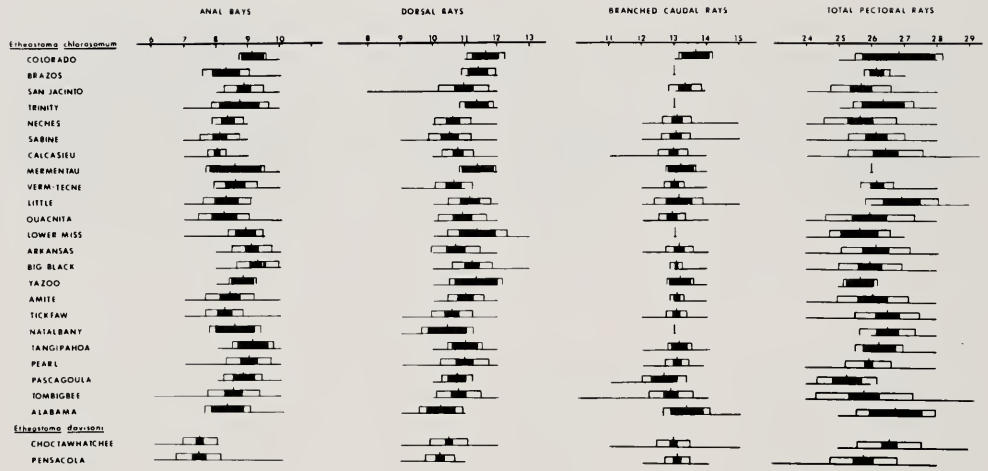

Fig. 3. Results of the graphical analysis showing variation in four ray count characters for Gulf Slope populations of *Etheostoma chlorosomum* and *E. davisoni*.

Colorado River population, variation in these characters was slight (Fig. 3). Scale meristics were less conservative (Figs. 4 & 5). Squamation showed the greatest amount of variation across the Gulf Slope (Figs. 6 & 7). Considerable variation was also observed in the lateralis system.

Conservative characters showed a consistent divergence in the Colorado River population, where the highest means for a number of these characters were recorded (Figs. 3, 4 & 5). The separation was significant in the case of caudal peduncle scale rows and branchiostegal rays (Fig. 10). The Brazos River population was also somewhat divergent with regard to scale count characters. In general, scale counts averaged higher in western populations, but the variation was clinal eastward to the lower Mississippi River drainage (Figs. 4 & 5). Fin ray and scale row characters did not support the separation of any other Gulf Slope populations of *E. chlorosomum*.

The pattern of variation in the lateralis system involved reductions in some populations. Considerable reduction was observed in the cephalic lateralis system (Fig. 2), resulting in confusion concerning the number of pores present and completeness of canals. In some instances canals were incompletely roofed or had large breaks, giving the appearance of additional pores. An analysis based on the number of pores present was meaningless under these conditions, and therefore was excluded.

Based on the pattern of variation of pored lateral line scales (Fig. 4), the reduction was most pronounced in lower Mississippi River basin, the Sabine River, and extreme eastern and western populations. Between these areas populations of *E. chlorosomum* showed a greater degree of lateral line development, a condition similar to that of *E. davisoni* (Fig. 4). The Choctawhatchee darter also showed complete development of the cephalic lateralis system (Howell, 1968).

The greatest degree of geographic variation was shown by squamation characters (Figs. 6 & 7). Squamation of the prepectoral region and anterior belly was complete for lower Mississippi River, and the adjacent Gulf Slope pop-

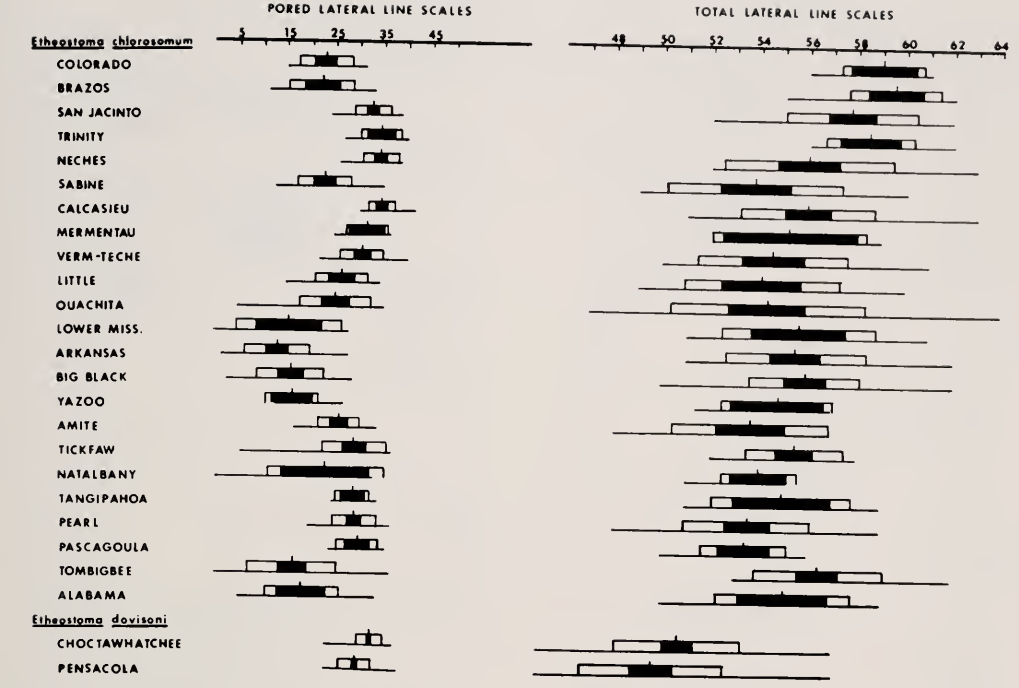

Fig. 4. Graphical analysis results for pored lateral line scales and total lateral line scales in Gulf Slope populations of *Etheostoma chlorosomum* and *E. davisoni*.

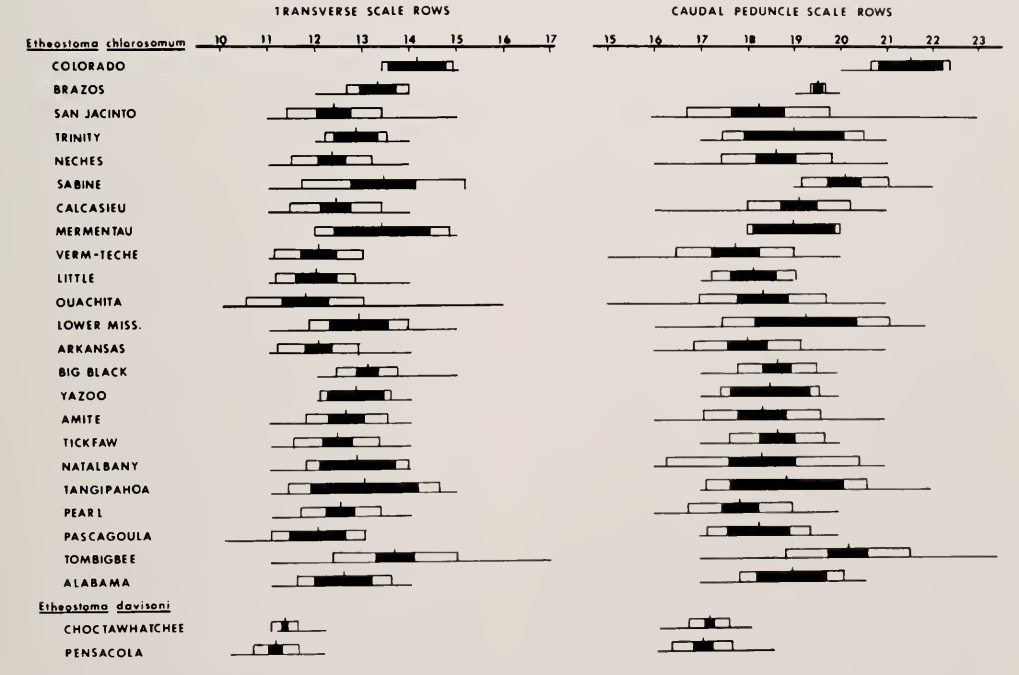

Fig. 5. Graphical analysis results for transverse and caudal peduncle scale rows in Gulf Slope populations of *Etheostoma chlorosomum* and *E. davisoni*.

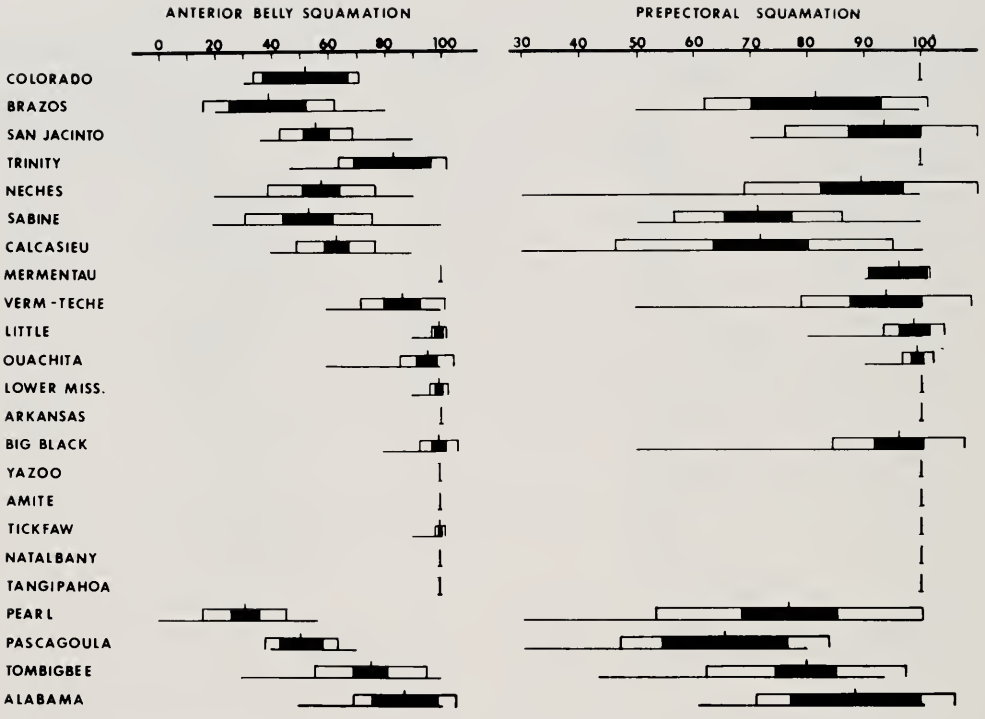

Fig. 6. Graphical analysis results for percent squamation of the anterior belly and prepectoral regions in Gulf Slope populations of *Etheostoma chlorosomum*.

ulations. We noted higher proportions of scales on the breast and nape for these populations as well. Variation in squamation was clinal west of the Mississippi River with gradual decreases in anterior belly squamation and more abrupt changes in prepectoral, breast and nape squamation. Higher squamation of the prepectoral, breast and anterior belly regions was observed west of the Neches River, primarily in the Trinity and Colorado River populations.

Step clines were observed east of the Lake Pontchartrain drainages for all squamation characters (Figs. 6 & 7). Pearl and Pascagoula river populations of *E. chlorosomum* had greatly reduced squamation. For extreme eastern populations in the Mobile Bay basin (Tombigbee and Alabama rivers), squamation was intermediate between that of lower Mississippi-Pontchartrain populations, and Pearl-Pascagoula populations. In general, the pattern was reversed east of the Pearl River and squamation increased clinally to a condition more similar to lower Mississippi populations. Figure 8 illustrates the pattern of squamation for a number of Gulf Slope populations of *E. chlorosomum*.

Page (1981) stated that character reduction was an important trend in darter evolution. Primitive darters in the genus *Percina* are characterized by higher mersitics and complete development of the lateralis system. These characters are often reduced in more derived forms. Howell (1968) assigned *E. davisoni* to the subgenus *Vaillantia* as a distant relative of *E. chlorosomum*. In characterizing the evolutionary divergence of these species, we assumed

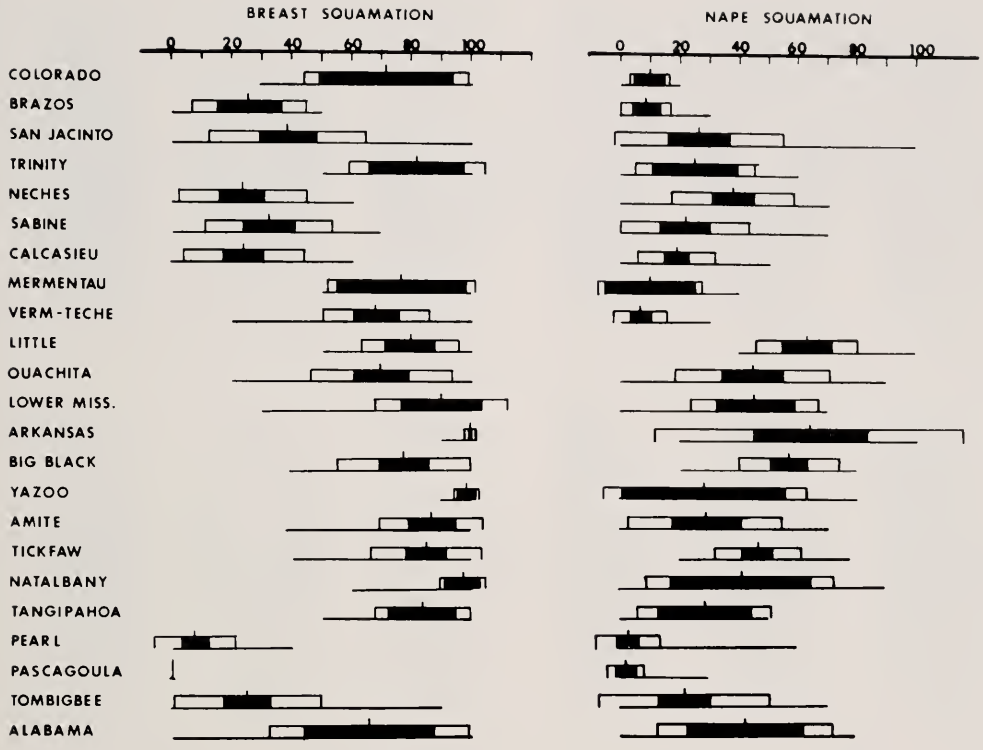

Fig. 7. Graphical analysis results for percent squamation of the breast and nape regions for Gulf Slope populations of *Etheostoma chlorosomum*.

that reduced character states represented the derived condition.

With respect to the characters analyzed in this study, ancestral *Vaillantia* characteristics apparently included complete squamation of the breast, prepectoral and anterior belly regions, complete development of the lateralis system, higher numbers of scale rows, fin and branchiostegal ray elements, and breeding tubercles. The divergence of *E. chlorosomum* apparently involved reductions in spiny ray elements (dorsal, anal and branchiostegal) and the cephalic lateralis system, while that of *E. davisoni* involved reductions in numbers of scale rows and squamation, and loss of breeding tubercles. The reduction in squamation observed for some Gulf Slope populations of *E. chlorosomum* is interpreted as subsequent to the divergence of the species. Squamation was more or less complete for presumed ancestral populations in the Mississippi River basin.

Sexual Dimorphism

Although male *E. chlorosomum* do not develop bright colors in the breeding condition, there was obvious sexual dichromatism. The bodies of breeding males were highly flecked with melanophores (more concentrated dorsolaterally) and heavy black pigment was observed on the interradial membranes of the spinous dorsal fin. Less intense pigmentation developed across the base and margin of the dorsal fin producing a flag like appearance which

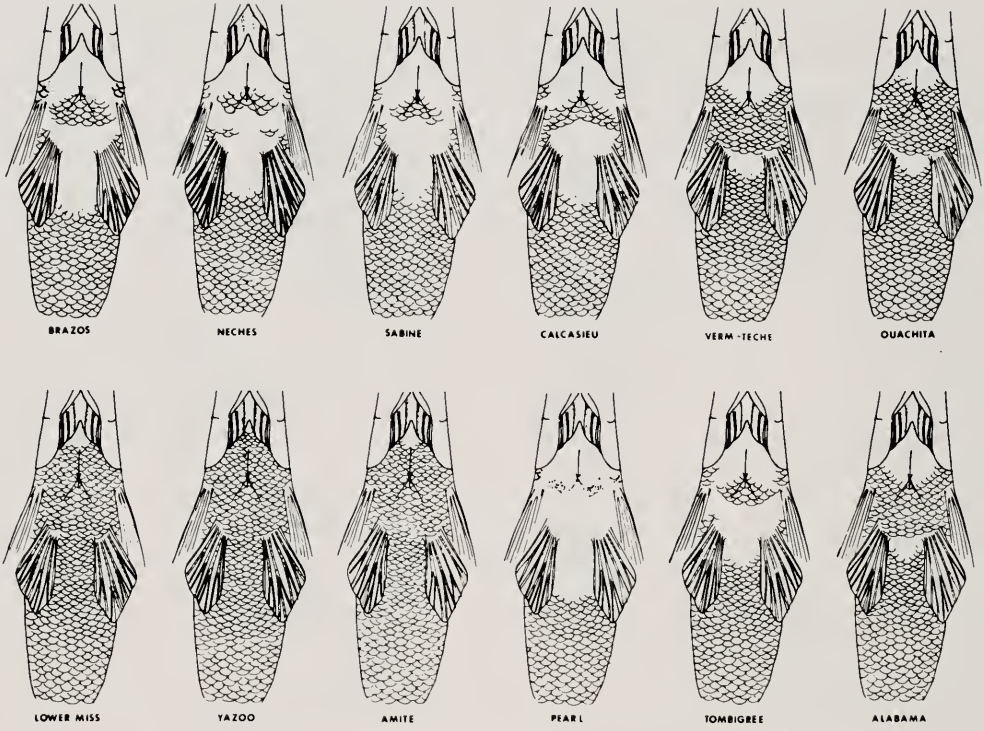

Fig. 8. Variation in squamation of the anterior belly and breast regions for a number of Gulf Slope populations of *Etheostoma chlorosomum*.

apparently serves for sexual or species recognition.

Sexual dimorphism was evident in a number of characters. Breeding males had small, tubular shaped genital papillae and thickened, fleshy pelvic and anal spines (Fig. 9). Tubercles were observed on the pelvic and anal fins of breeding males but showed considerable variation in development. Tubercles were usually seen on the anterior rays of these fins but in some instances occurred on all rays and the spine (Fig. 9a). There was no geographic pattern to the variation in tubercle development. Females had large, fleshy, heart-shaped genital papillae, which increased in size as they approached the height of the breeding condition (Fig. 9d & e). In most areas, females retained normal, nonbreeding coloration in the breeding condition.

Mature males and females had two rows of tubercle-like structures on the interradial membrane of the caudal fin. These structures apparently differ from the tubercles observed on the caudal rays of males darters in the subgenera *Ericosoma*, *Imostoma*, *Ammocrypta*, and *Etheostoma* (Collette, 1965). Their distribution and fleshy nature, however, suggests a function similar to contact organs during spawning. Examination of *E. davisoni* revealed similar structures with an identical distribution on the caudal fin. Males had higher numbers of scale rows around the caudal peduncle and greater anterior belly and prepectoral squamation (Table 1). On the average males were larger than females, suggesting that the differences were size related. Both sexes were equally represented in the population samples to

reduce bias resulting from sexual variation.

Discussion

The patterns of variation in *E. chlorosomum* were similar to those observed by Burr (1978) for the cypress darter, *E. proeliare,* a species with a distribution similar to that of *E. chlorosomum.* Burr (1978) described the following patterns of geographic variation: 1) variation slight and random; 2) unusual variation in certain drainages; and 3) Gulf Coast populations in Texas somewhat divergent. However, in *E. chlorosomum* most slight and randomly variable characters showed a consistent divergence in the Colorado River population. The bluntnose darter was recorded west of the Colorado River, in the San Antonio Bay drainage (Gilbert, 1980), although the material on which this record was based no longer exists (Clark Hubbs, pers. comm.). These extreme western populations may warrant special taxonomic consideration. Attempts to collect additional material from these drainages, however, have been fruitless thus far.

Clinal variation was observed in populations west of the Mississippi River. Clines were seen in gradually changing characters such as lateral line scales (Fig. 4) and anterior belly and breast squamation (Figs. 6 & 7). These characters, together with pored lateral line scales, were important in establishing the limits of subspecies in previous studies of percid species. The clines originated in the lower Mississippi and continued westward to the Brazos River population. The divergence noted in the Trinity River for squamation may be attributed to small sample size. A similar shift was seen for the Mermentau River population, which was also based on a small sample.

Reductions in the lateralis system did not follow a clear geographic pattern. Considerable reduction was observed for the Colorado, Brazos, Sabine, lower Mississippi, and Mobile Bay populations. The trend was best illustrated by variation in pored lateral line scales (Fig. 4), with the above populations showing distinctly lower numbers of pored lateral line scales. The peculiar pattern involved extreme western populations which were divergent in other respects, extreme eastern populations which were somewhat intergraded in other respects, central Gulf Slope populations (lower Mississippi), and the Sabine River population.

Information from other darter studies suggests that reduction in the lateralis system may be environmentally induced. Significant reductions in the system were observed for darters in the subgenera *Hololepis* (Hubbs and Cannon, 1935; Collette, 1962), *Catonotus* (Page and Braasch, 1976), and *Microperca* (Burr, 1978). Burr (1978) suggested that the reduction was correlated with ecological parameters. In the three groups mentioned above, the species showing the greatest reduction in the lateralis system were associated with quietwater habitats (swamps, low gradient streams, springs and lakes). The populations of *E. chlorosomum* showing the trend were from large, sluggishly flowing river systems. The habitat of the bluntnose darter in these systems is described as quiet backwaters, oxbows and sloughs (Pflieger, 1975). Additional comparisons of populations from large versus small streams or quiet vs. running water habitats are needed before it can be determined whether development of the lateralis system is environmentally controlled. However, such an explanation seems more plausi-

ble than one based on genetic relationships.

Nape squamation (Fig. 7) produced irregular clines with rather abrupt changes between the Vermilion-Teche and the lower Mississippi, the boundary between the western Gulf Slope and the Mississippi River basin. All squamation characters showed abrupt changes in the Pearl and Pascagoula populations. The differences were significant in some instances. The results suggest that eastern populations stabilized at greatly reduced squamation due to isolation from the fully scaled central stock found in the Mississippi River and its tributaries. These populations were similar or slightly variable in other respects.

There was evidence for isolation between the Pearl River population and populations in and around the lower Mississippi River based on variation in squamation. However, squamation was variable and intermediate in the Mobile Bay basin populations to the east, suggesting intergradation between populations with greatly reduced squamation (Pearl and Pascaqoula), and those populations with high to complete squamation (Mississippi and its tributaries).

Populations of *E. chlorosomum* could have gained access to the Mobile Bay drainage via the Big Black, Yazoo, or other more northern Mississippi River tributary. The distributions of a number of other species, most notably, *E. nigrum*, reflect this type of dispersal pattern; occurring in the lower eastern tributaries of the Mississippi River and the Mobile Bay basin, but not in the intervening coastal drainages. The decline in squamation from the Alabama River westward to the Pearl River suggests separate invasion of the Mobile Bay basin from the west (via the Pascagoula

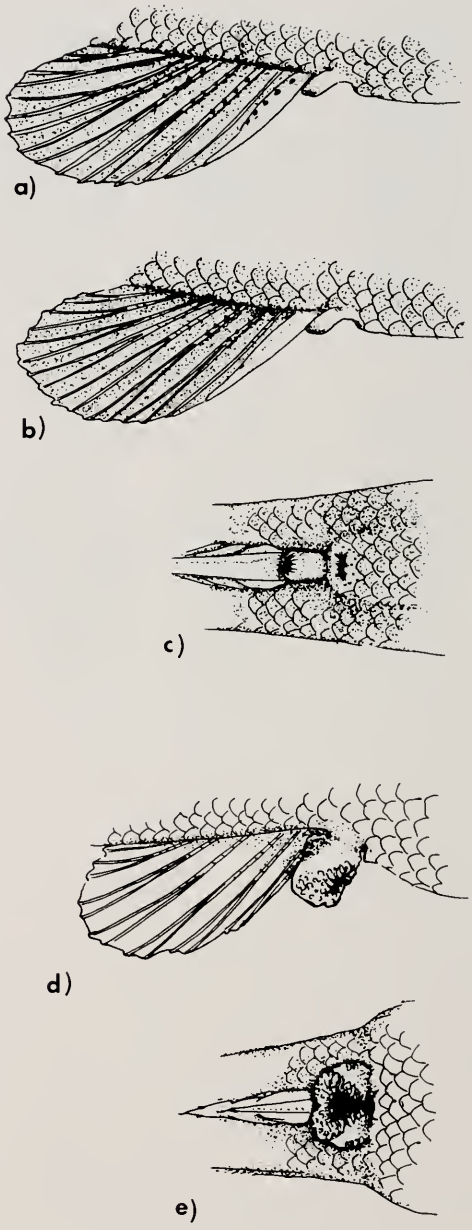

Fig. 9. Sexual dimorphism in Gulf Slope populations of *Etheostoma chlorosomum:* a-c) Male breeding condition showing tubular genital papillae, thickened (fleshy) anal spine and development of tubercles on anterior rays on the anal fin or on all rays and the spine. d & e) Lateral and ventral view of the large heart shaped genital papilla of breeding females.

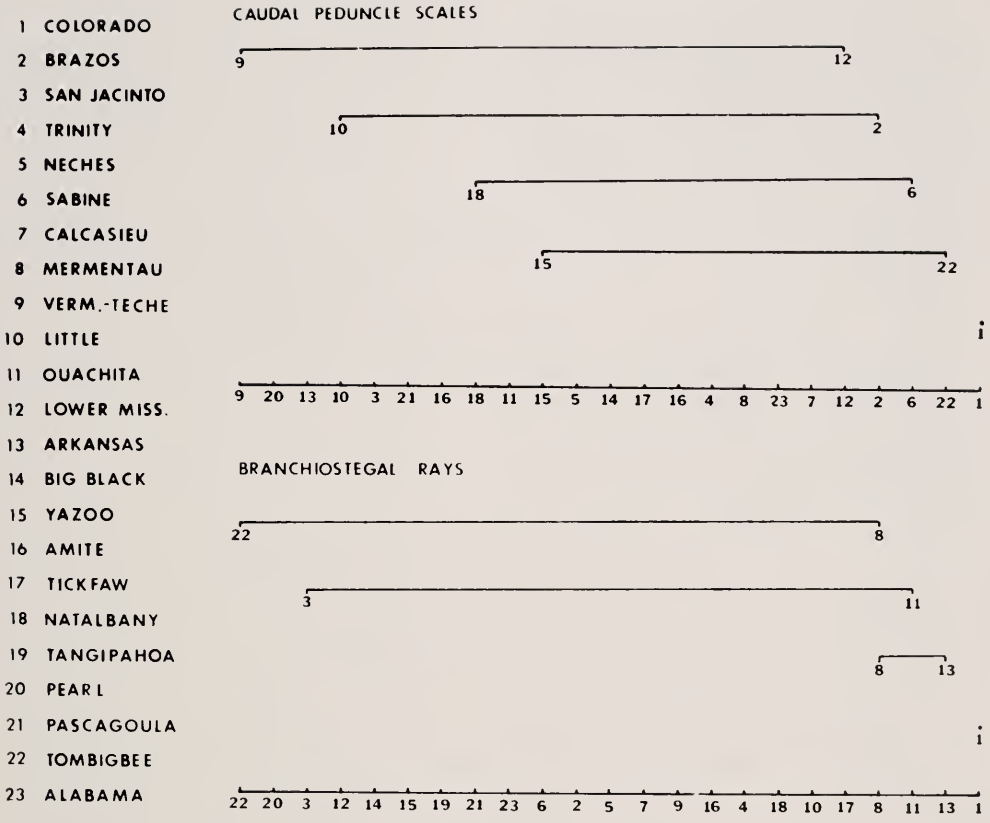

Fig. 10. Results of the SNK multiple range test for caudal peduncle scale rows and branchiostegal rays showing divergence for the Colorado River population. Numbers below subsets and ranges correspond to numbered drainages (populations) on the left.

River) and subsequent exchanges between these populations.

Results of the multiple range test indicated considerable overlap for most groups, but similar patterns of variation emerged (Figs. 8-9). The Colorado River population was distinct in the number of branchiostegals and caudal peduncle scale rows (Fig. 10). The Pearl and Pascagoula populations were distinct with respect to percent squamation of the anterior belly and breast (Fig. 11). The Tombigbee and Alabama populations were intermediate between the Pearl and Pascagoula, and the lower Mississippi and Pontchartrain populations for these characters.

Causes of Variation

Of particular importance to the interpretation of geographic variation is distinguishing between nongenetic causes of phenotypic variation (direct modification by the environment, sexual variation, and developmental variation) and causes of true genetic variation. Causal factors of true genetic variation include selection, random genetic drift, founder effect, and on a short temporal scale, recent migration without time to adapt to local conditions (Gould and Johnston, 1972).

There are no pronounced environmental differences between Gulf Slope drainages that would offer a high adap-

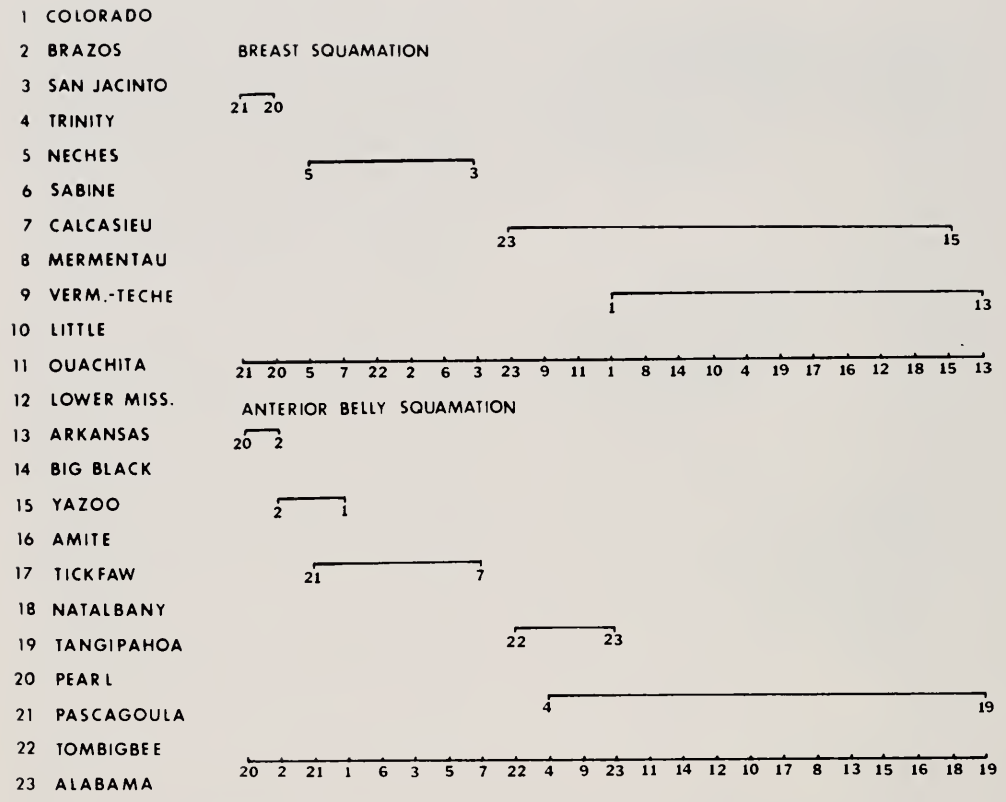

Fig. 11. Results of the SNK multiple range test for anterior belly and breast percent squamation showing the isolated nature of the Pearl River population.

tive value to the divergent character states observed for some *E. chlorosomum* populations. If these divergent character states resulted from true genetic variation it is more likely that they were the product of random genetic effects.

Most discussions of environmental factors that produce morphological variation in fishes deal with temperature effects in northern versus southern populations of a species. In this study east-west variation was analyzed in populations distributed across a relatively homogeneous (humid subtropical) climatic region. Thus, the variation in meristic elements observed here is not readily explained by the effects of temperature on growth rates. Other growth retardants such as high salinity or low dissolved oxygen, which parallel the effects of temperature (Barlow, 1961), may operate along the Gulf Slope. The role of these factors in producing the observed variation is not known.

Pflieger (1971) suggested that the bluntnose darter evolved in the central Mississippi River Valley. Presumably, the species then spread east and west along the Gulf Slope where it colonized new habitats. Hubbs (1928) stated that a species new to an area would be altered by the environment and these differences, when associated with adaptive changes would become genetically fixed. Based on the high degree of variability in the patterns of variation observed, it appeared that of the many characters analyzed, few were geneti-

cally fixed in Gulf Slope populations of *E. chlorosomum*. Instead, there was evidence of varying degrees of isolation and intergradation.

The variation observed was not explained by sexual differences. Although a few important characters showed significant differences between sexes (Table 1), character trends were not disturbed by combinations of data from different sexes as long as both were equally represented. An attempt was made to avoid the effects of ontogenetic variation by restricting examinations to individuals presumed to be adult sized. Collette (1962) suggested that variation in the lateralis system was developmental for members of the subgenus *Hololepis*. However, based on the pattern of variation observed here and elsewhere (Burr, 1978), development of the lateralis system appears to be environmentally controlled.

According to Barlow (1961) characters that are the last to develop ontogenetically are more adaptable. Collette (1962) noted that scales originate in the caudal peduncle region and then spread anteriorly during the early development of *E. fusiforme*. The last areas to develop scales were the nape, belly, breast and head (Collette, 1962). Squamation characters showed high degrees of reduction across the Gulf Slope range of *E. chlorosomum* and little variation (from the fully scaled state) in the Mississippi River basin. These character states probably originated ontogenetically, but they showed true genetic variation in Gulf Slope populations of *E. chlorosomum*.

Zoogeography and Evolution

The distribution of extant *Vaillantia* species suggests that the common ancestor of the group occupied lowland areas

TABLE 1. Sexual variation among lower Mississippi populations of *E. chlorosomum*. Significance determined by t test. Probabilities (P) greater than 0.05 nonsignificant (ns).

		Sexual variation				
Character	Sex	X	SD	N	t	p
Standard length	M	37.49	3.61	42		
					3.70	<.005
	F	34.51	3.16	33		
Total l.l. scales	M	59.11	2.26	4		
					1.29	ns
	F	59.67	1.12	33		
Pored l.l. scales	M	23.44	5.90	42		
					1.22	ns
	F	21.67	6.44	33		
Caudal peduncle	M	20.44	1.15	42		
					1.95	<.05
	F	19.89	0.60	33		
Anterior belly	M	47.78	19.86	42		
					1.93	<.05
	F	37.78	24.38	33		
Prepectoral	M	96.67	7.07	42		
					4.96	<.005
	F	78.89	21.47	33		
Nape	M	10.00	10.00	42		
					1.17	ns
	F	7.78	4.41	33		
Breast	M	43.33	26.46	42		
					0.61	ns
	F	38.89	35.86	33		

of the Gulf Coastal Plain, including the Mississippi River Valley and the eastern *Gulf Slope*. *E. davisoni* is restricted to Gulf Slope drainages east of Mobile Bay. Bailey et al. (1954) stated that due to isolation, drainages east of Mobile Bay form a common faunal block that was predominantly derived from the Mississippi River. Evidence from this study suggests long-term isolation of *E. davisoni* from its presumed ancestor in the Mississippi River, and a more recent history for *E. chlorosomum* in Gulf Slope drainages east and west of the Mississippi River.

Most of the present Gulf Coastal Plain (including the Mississippi Embayment up to the southern lowlands of Missouri and Kentucky) was below sea level until the late Oligocene. A precipitous drop in sea level occurred during that period (Vial and Hardenbol, 1979), which could have exposed the region to colonization by primary freshwater fishes for the first time. We hypothesize that the common ancestor of *E. chlorosomum* and *E. davisoni* was a lowland form, autochthonous to the Mississippi River basin, that attained a widespread Gulf Coastal distribution in late Oligocene or early Miocene times. *Etheostoma davisoni* likely evolved from ancestral *Vaillantia* populations that were isolated in Gulf Slope drainages east of Mobile Bay during the middle Miocene, when a sustained, 100 m elevation in sea level caused reflooding of the Mississippi Embayment (Vial and Hardenbol, 1979). A marine transgression of this magnitude could have also restricted ancestral populations to northern areas of the Mississippi Embayment; the presumed area of origin of *E. chlorosomum* (Pflieger, 1971). The isolation of ancestral *Vaillantia* populations that produced the extant species may have occurred more recently, as a result of a subsequent transgression (similar in magnitude, but much shorter in duration) in Pliocene times (Vial and Hardenbol, 1979).

The bluntnose darter most likely invaded Gulf Slope drainages during glacial periods when heavy precipitation caused high degrees of flooding (Bailey et al., 1954), crossgrading (Distler, 1968) and headwater stream captures (Burr, 1978; Conner, 1977) in the region. Regression of sea water during glacial maxima, coupled with increased deposition in large rivers may have also allowed transfers of primary freshwater fishes across bays and bayous into adjacent drainages (Conner, 1977).

Burr (1978) stated that *E. proeliare* may have used a lowland transfer to enter the Pearl River from the Mississippi River in fairly recent times. An earlier transfer from lower eastern tributaries of the Mississippi River, such as the Big Black (Snelson, 1972; see also Suttkus and Clemmer, 1977), seems more likely for the Pearl River population of *E. chlorosomun* due to its isolated nature.

Lake Pontchartrain was suggested to have been isolated as a totally freshwater basin at least once during its formation as the Mississippi River flowed eastward along the St. Bernard Delta (Saucier, 1963). Populations of *E. chlorosomum* in the Pontchartrain drainages were similar to lower Mississippi River populations in a number of respects.

Burr (1978) cited evidence for stream captures between eastern tributaries of the Mississippi River and western tributaries of the Tombigbee River which could explain the entrance of *E. chlorosomun* into the Mobile Bay basin. Extant populations in the Mobile basin were apparently intergraded with

divergent stocks from the Pearl and and Pascagoula Rivers.

To the west, clines indicated a more gradual divergence of populations. The distribution of *E. chlorosomum* was more continuous west of the Mississippi River, suggesting a higher degree exchange and intergradation in the past. The spread of *E. chlorosomum* westward along the Gulf Coast could be explained by any of the above mentioned processes. Burr (1978) favored lowland transfers of *E. proeliare* west of the Mississippi because the species was only known from lower portions of western Gulf Slope drainages. The same may have been true for *E. chlorosomum* which has a similar distribution west of the Mississippi River. Transfers via captures or cross-graded streams may have occurred as well (Distler, 1968). Conner (1977) cited evidence for Kansan and preKansan glacial period captures between the Red and Brazos rivers and the Colorado and Brazos, which could explain the spread of *E. chlorosomum* to these far western areas.

Taxonomic Conclusions

We found little evidence to support the taxonomic recognition of any group of *E. chlorosomum* populations from the Gulf Slope region. Instead, we observed: 1) conservative variation (slight and random) for some characters; 2) evidence of isolation and intergradation in some populations for characters that were adaptable; and 3) evidence for enviromental control of variation in other characters. Extreme western populations were divergent for important, (otherwise conservative) characters. However, an insufficient amount of material was available to make a definite conclusion regarding their status.

Based on the patterns of variation observed in comparisons among *E. chlorosomum* populations and between *Vaillantia* species, adaptable characters such as those from the lateralis system and body squamation would have a questionable value in taxonomic decisions below the genus level. Adaptation or random fixation of new states was better suggested by variation in characters that were otherwise more conservative.

Acknowledgments

We wish to extend special thanks to W. Michael Howell, Samford University, for his willingness to share his extensive data on *E. chlorosomum* and *E. davisoni,* and other contributions to this study. James S. Rogers provided guidance on the use of statistical techniques, and Eugene C. Beckham, Brooks M. Burr, John V. Conner, Clark Hubbs, Lawrence M. Page, and Michael M. Stevenson provided distributional records and helpful comments. This acknowledgement is not meant to imply agreement with the conclusions reached by the authors.

For allowing us to examine museum material under their care, we wish to thank: Herbert T. Boschung, University of Alabama (UAIC); Ed Brothers, Cornell University (CU); Neil H. Douglas, Northeastern Louisiana University (NLU); Clark Hubbs, Robert D. Martin and Doyle Mosier, University of Texas Natural History Collection (TNCH); and Royal D. Suttkus, Tulane University, Museum of Natural History (TU). The vertebrate collection at the University of New Orleans (UNO) was also utilized.

We would also like to thank Janet Forbes for typing drafts of the manuscript.

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